THE DISTRIBUTION OF ALLOGROOMING AMONG FEMALE JAPANESE MACAQUES (*MACACA FUSCATA YAKUI*)

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I certify that this thesis is the true and accurate version of the thesis approved by the examiners

Signed ..[redacted]..... Date..22/06/07

(Director of Studies)

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LIST OF PAPERS PUBLISHED USING THE DATA COLLECTED FOR THIS THESIS (SEE APPENDIX A AT THE END OF THE THESIS FOR A COPY OF EACH PAPER)

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THESIS ABSTRACT

Allo-grooming is the main behaviour primates use to establish and maintain amicable social relationships and, for this reason, it has been intensively studied in the last three decades. Notwithstanding this, conclusive data on the factors affecting allo-grooming distribution and on its benefits are still scarce. This Thesis thus aimed to analyse the importance of the following factors in the distribution of allo-grooming among female Japanese macaques (*Macaca fuscata yakui*): environmental variables, seasonal changes in food abundance and group size. This study also aimed to analyse some possible benefits of allo-grooming, namely, the reciprocation of allo-grooming (considered to be beneficial for the removal of parasites), tolerance over food and agonistic support. Data were collected on 28 females living in two groups of different size (N = 21 and around 50, respectively), on Yakushima Island, Japan.

Allo-grooming was not affected by ambient temperature or relative humidity, suggesting that this behaviour is so important for the maintenance of amicable social relationships that it became independent from environmental variables (while this did not happen for behaviours related to pelage care but lacking any social function, such as self-grooming). Allo-grooming distribution and reciprocation were unaffected by seasonal changes in food abundance. Conversely, group size affected allo-grooming: females in the large group spent more time allo-grooming and were more selective in their choice of grooming partners. Finally, allo-grooming increased the chances of agonistic support against a male aggressor and it also favoured tolerance near food sources. The findings of this Thesis indicate that allo-grooming is relatively resilient to mild, short-term changes of habitat characteristics, while it may be affected by group size. They also highlight the importance of this behaviour for the establishment and maintenance of amicable social relationships and for obtaining social benefits (e.g. tolerance) other than allo-grooming itself.

CHAPTER 1

SOCIAL RELATIONSHIPS AND GROOMING DISTRIBUTION IN THE PRIMATE ORDER

1.1 Brief Overview of the Thesis.

Stable and long-lasting amicable social interactions between group members are one of the features of primate social behaviour. Such relationships are mainly established and maintained through allo-grooming exchange (referred to as grooming, in the rest of the Thesis), defined as an interaction between two or more animals during which the monkeys carefully pick through and/or slow brushes aside the fur of another individual with one or both forepaws (Rosenblum *et al.*, 1966). The possible benefits of grooming interactions are thought to be reduced parasite load or increased agonistic support, tolerance over food sources or other limited goods (e.g. Dunbar, 1991). In the last few decades, many observational and theoretical studies have analysed the factors affecting the distribution of grooming, its effects on individual fitness, and the strategies that primates follow to establish and maintain social relationships. However, this topic is still a matter of great debate and many further studies are required to clarify it.

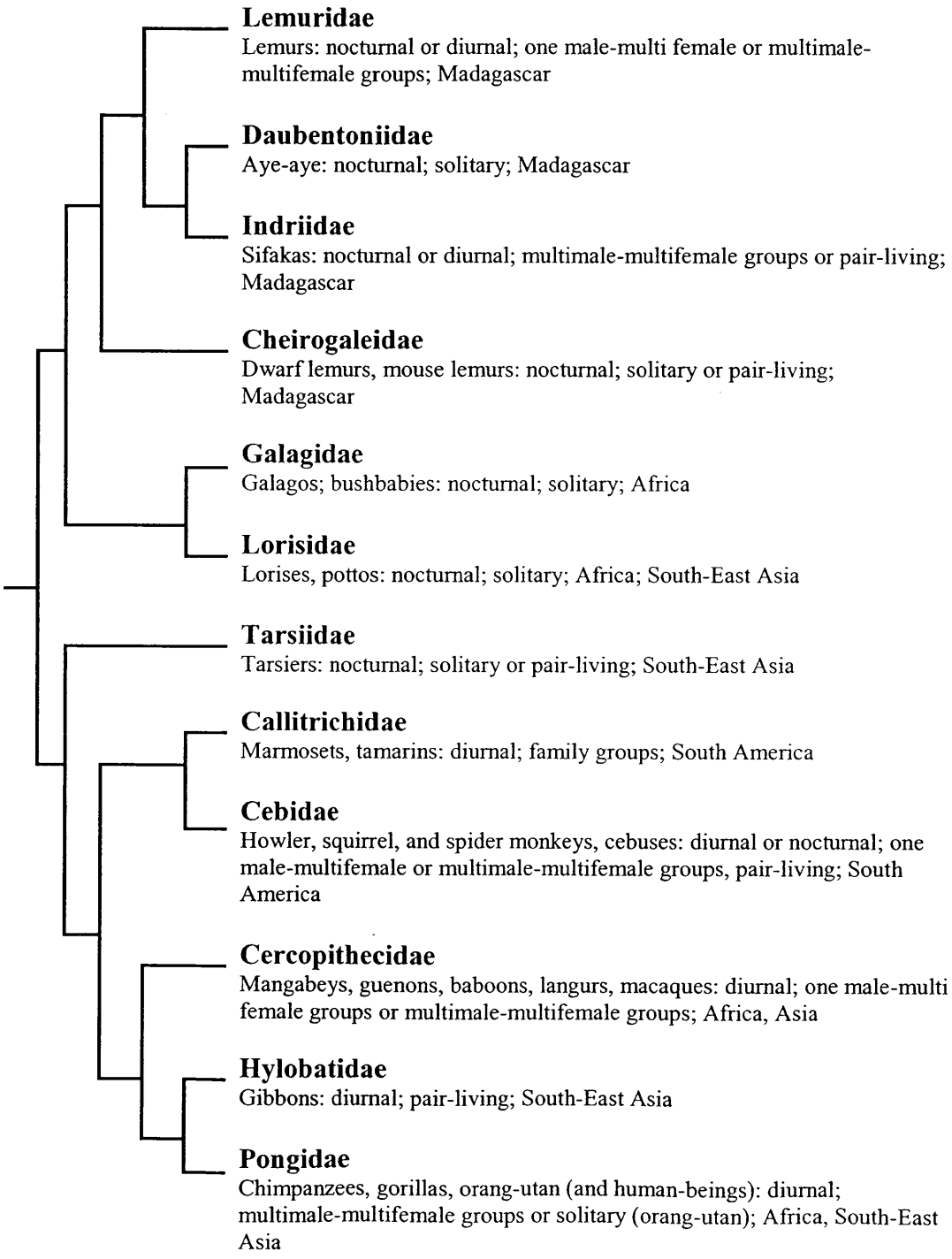
This Thesis analyses the distribution of grooming among female Japanese macaques (*Macaca fuscata yakui*) living in two groups on Yakushima Island, Japan. Yakushima macaques spend a great proportion of the day in grooming interactions and, thus, represent an ideal species to study this behaviour. The Thesis aims to determine the importance of the social and non-social factors affecting grooming distribution and the possible benefits of grooming. The following sections of this chapter contain an overview of the theories proposed to explain the evolution of social behaviour in primates and the distribution of grooming, and to discuss the various models analysing grooming exchange. Moreover, the following sections also include some general information on the behavioural ecology of Yakushima macaques, and the specific aims of this Thesis.

Chapter 2 provides details on the animals, the study site, and on the methods of data collection used in this Thesis. Chapters 3 to 7 contain the results, and Chapter 8 a general discussion on the findings of this Thesis in light of our current knowledge of the topic, possible methodological improvements and further lines of research.

1.2 The Evolution of Sociality in the Primate Order.

The Primate Order includes human-beings and our closest relatives (see Figure 1.1) Solitary and nocturnal life is considered the ancestral social organisation of early primate species and it is still observed, although at different degrees, in some "lower" primates such as lorises and bush-babies (Fleagle, 1999). Some primate species, however, form the most complex societies observed in the animal kingdom, comparable to only a few other non-primate species (e.g. whales, dolphins and elephants; Mann *et al.*, 2000; Moss, 1988). Moreover, from a comparative point of view, primate social organisation and behaviour may help us to understand both primitive and modern human societies (e.g. Barrett *et al.*, 2002a). For these reasons, the evolution of sociality in the primate order is a topic that has attracted, and still does so, a great number of students interested in analysing the costs and benefits of group living (e.g. Clutton-Brock and Harvey, 1976; Crook and Gartlan, 1966; Trivers, 1985). Despite this interest, the relative importance of factors shaping group living is still a matter of great debate (Johnson *et al*, 2002; Kappeler and van Schaik, 2002). Indeed, all the theories proposed so far differ from one another in the relative importance that the authors attribute to the ecological factors that shape social behaviour. However, all the authors agree that social life may be seen as attempts by individuals forming the groups to maximise their inclusive fitness (see Table 1.1; Hamilton, 1964). The type of social organisation of a species is affected by the energetic requirements and reproductive tactics of group members. This view is based on Trivers's assumption that males and females differ with respect to the factors that may affect their fitness (see Table 1.1; Trivers, 1972). The reproductive success of

Figure 1.1: Basic primate phylogeny based on fossil, molecular and karyotypic data (Purvis, 1995). For each family (in bold), the common names of some genera are given, together with their most common activity patterns (nocturnal or diurnal) and social organisation, and the geographic distribution. The cladogram represents true phylogenetic relations among taxa but not temporal divergences.



female primates is mostly affected by food quality and abundance, given the energetic costs of lactation and the relatively long-lasting parental care. In contrast, male reproductive success mostly depends on winning competition for mating partners. As such, female social behaviour and grouping patterns are considered to be a direct consequence of the habitat characteristics (e.g. food distribution) while male behaviour is thought to depend on the number and distribution of females in a given area. In other words, female response to environment seems to be the driving force of primate social evolution (Lindenfors *et al.*, 2003). Based on these considerations the theories proposed for the evolution of group living in primates pay particular attention to female relationships.

a) Wrangham and van Schaik theories on group-living in primates.

Food competition is usually distinguished as indirect (scramble) competition, when some animals remove limited food supplies from an area before other group members can feed, and direct (contest) competition, when high-ranking individuals monopolise access to food or when animals fight over a food item (van Schaik and van Noordwijk, 1988). These two types of competition (both intra- and inter-group) are often found together and their relative importance varies across species and even among populations. More than 20 years ago, Wrangham (1980) proposed that group living is favoured when inter-group contest competition for food is high, as larger groups defend food sources from competing groups better than smaller ones or single individuals. This author also considered that predation pressure is relatively irrelevant in shaping social patterns. The theory goes on, predicting that when food is clumped (i.e. defensible) and of high energetic value females should be phylopatric, form matrilines and show coalitions against foreign groups and/or within the single matriline in order to defend food sources. Conversely, when food is dispersed and of low quality female transfer may appear and coalitions among females and inter-group contest food competition should be low.

In a series of papers, van Schaik and colleagues (van Schaik, 1983, 1989; Sterck *et al.*, 1997) partially challenged this view. They argued that group living

evolved mainly as a response to predation pressure, as large groups should pinpoint predators or defend themselves from them more effectively than small groups or individuals alone (e.g. Dunbar, 2002; Hill and Dunbar, 1998; Isbell *et al.*, 2003). Indeed, groups are more cohesive and inter-individual distances shorter when predation pressure is high (Barton *et al.*, 1996; Hamilton, 1971). This second theory recognised the importance of food competition as an important factor affecting social behaviour but considered it as secondary with respect to predation pressure.

b) Additional factors shaping social behaviour in primates: foraging efficiency, infant care and infanticide.

Other factors than food or predators may potentially favour group living. Foraging efficiency (see Table 1.1) is expected to be higher in social animals as group members have more chances to detect clumped and/or concealed food than individuals alone (see Ruxton and Glasbey, 1995 for a theoretical approach). Improved care-giving opportunity is one additional factor that may have promoted the evolution of sociality (Dunbar, 1988): group living mothers may receive some help from other individuals (in the form, for example, of infant carrying during group movement); this is not possible for solitary mothers (e.g. polar bear). Allo-parental behaviour may occur among genetically-related group members but also between unrelated individuals (Hoage, 1978; Tardif, 1997). Recently, male reproductive strategies have been recognised as important determinants of primate social organisation, particularly in relation to male ability to commit infanticide (van Schaik *et al.*, 1999). In many species (e.g. langurs: Blaffer-Hrdy, 1979; chimpanzees: Goodall, 1986; common marmosets: Digby, 1995), males have been often observed attempting to kill infants of lactating females in order to stimulate the resumption of oestrus in those females. Infanticidal males are usually foreign or subordinate animals who have recently attained the alpha position in a group (e.g. Soltis *et al.*, 2000) and thus are unlikely to have sired the new-born infants of that group. As expected, large groups containing many lactating females attract more infanticidal males than small groups (Nunn and van Schaik 2000; Steenbeek and van Schaik, 2001). As a consequence of this, females living in large groups

may try to exclude other females from the group or transfer to small groups to reduce the risk of infanticide (Steenbeek and van Schaik, 2001). Moreover, lactating females may form coalitions against infanticidal males in order to reduce the risk of the infants being killed (Blaffer-Hrdy, 1979; Soltis *et al.*, 2000). These observations indicate that male reproductive behaviour and female counter-strategies are important factors that may affect adult sex ratio (see Table 1.1) and the types of social interactions within and between groups (van Schaik and Janson, 2000).

c) Social relationships and cognitive constraints on social behaviour.

Early primatologists recognised that primates living in the same group are capable of maintaining long-lasting social relationships with one another (Imanishi, 1960). The capacity to form such relationships can only evolve when some conditions are met (Cheney and Seyfarth, 1999; Hinde, 1976). First, animals have to have a minimum amount of time to devote to social interactions during the day. Second, group members have to live and remain in the same group long enough to build up and maintain long-lasting social relationships with one another. Third, animals have to individually recognise and remember each group member. Fourth, they need to remember the quality (i.e. aggressive or amicable) of their social relationships with the other group mates. Fifth, some knowledge of the type of social interactions that other group members maintain with one another may be advantageous to discriminate which companion may be a "friend" or not (Cheney and Seyfarth, 1990a, b; van Schaik and Deaner, 2003). There is now supporting evidence (see Cheney and Seyfarth, 1990b for a review) that these conditions are met by "higher" primates (i.e. Old and New World monkeys, and apes; see Figure 1.1). The quality of a relationship between two animals is characterised by its value ("what the subject gains from her/his relationship with a partner"), its security ("the perceived probability that the relationship with the partner will change"), and its compatibility ("the general tenor of social interactions in a dyad"; Cords and Aureli, 2000: p. 178). In light of these considerations, it has been proposed that each primate has an upper number of animals, related to the cognitive capacities of the species, about whom she/he is

capable of gathering and memorising sufficient information on the social interactions they have one another or share with itself (Barton and Dunbar, 1997). As such, group size and the type of social interactions among group members also depend on the cognitive capacities of a species (Barton, 1996; Dunbar, 1996). In other words, when group size increases beyond a given point (which depends on the specific cognitive capacities of a species), due for example to a long period of food abundance, groups become socially unstable as animals are unable to maintain cohesive movements and social relationships with all their group companions.

In synthesis, infanticide avoidance and defence from predators currently appear to be the main factors that led to the evolution of group-living in many primates (and probably in other social species). This does not mean, however, that no other factors were involved in this evolutionary process. Indeed, sociality may give additional benefits to individuals, including defence, or better detection of food sources. It is thus possible and perhaps likely that group-living triggered a series of evolutionary "responses" in primates, such as larger brains, to cope with a more complex social and socio-ecological environment (Tattersall, 1998).

1.3 The Importance of Grooming for Social Primates.

Since researchers discovered that primates devote a considerable amount of time each day to social behaviour it became evident that grooming is the most common affiliative behaviour (Sparks, 1967). This behaviour has been intensively studied by primatologists in the last few decades (e.g. Dunbar, 1991). Grooming is considered to have some associated costs, as it is a time-consuming activity. Moreover, macaque mothers involved in grooming interactions reduce the level of vigilance towards their infants (Cords, 1995; Maestripieri, 1993). Finally, grooming exchange requires very short inter-individual distances between the interacting animals, which, in turn, may increase the likelihood of aggression (see below). Therefore, attempts by lower-ranking animals to groom higher-ranking ones may potentially result in conflicts. Despite this risk, grooming tends to be

directed up the hierarchy in many primate species (Schino, 2001; for an example on non-primates see Kutsukake & Clutton-Brock, 2006). To reduce the risk of receiving aggression, however, lower-ranking animals tend to groom the back of animals ranking higher than themselves as a method to avoid eye contact with them (a common sign of aggressive intentions in many primates; Boccia *et al.*, 1982; Moser *et al.*, 1991). However, a negative relationship exists between time spent foraging and resting whereas no such relationship is found between foraging and grooming (Dunbar and Sharman, 1984). As such, grooming is conserved in the face of other demands (e.g. increased foraging requirements), despite being costly. For all these reasons grooming is considered to be an altruistic behaviour (Cheney and Seyfarth, 1990; Kurland, 1977; Seyfarth and Cheney, 1984; 1988). Altruistic acts can be evolutionary stable through kin selection (Hamilton, 1964; see Table 1.1) or if the recipient reciprocates the service obtained to some extent (Trivers, 1971; see Section 1.4).

Grooming presumably evolved as a means to reduce parasite loads and the risk of infectious diseases, and to remove the dirt from the fur (Freeland, 1981; Tanaka and Takefushi, 1993). Primates tend to receive grooming to parts of their body that they cannot reach through self-grooming and that thus would be more at risk of parasites if they exchanged no grooming with the other group members (Barton, 1985; Hart, 1990; Tanaka and Takefushi, 1993). Based on this observation, it was originally postulated that grooming has mainly a hygienic function (Hutchins and Barash, 1976). Contrasting this view, some authors speculate that the amount of time that primates devote to grooming is too great to be solely explained by its hygienic function (Boccia, 1983; Dunbar, 1991). Many observational studies have predicted the possible functions of grooming. These studies may be grouped into two main hypotheses, not mutually exclusive: the first hypothesis postulates that grooming has a tension reduction function, while the second hypothesis (or, more correctly, group of hypotheses) highlights the importance of grooming as a way to obtain various social benefits.

a) Grooming as a tension reduction mechanism.

Physiological studies, mainly conducted on macaque species, indicate that both heart rate and the occurrence of stress-related behaviour decrease in the groomees (i.e. the animals receiving grooming) during and immediately after a grooming session (Boccia *et al.*, 1989; Schino *et al.*, 1988; Terry, 1970). Moreover, grooming also increases the level of beta-endorphin in the blood, an opioid that reduces the level of stress (Keverne *et al.*, 1989). The tension reduction function of grooming also emerges immediately before or during contexts that are thought to increase social tension (de Waal and Hoekstra, 1980; Judge, 2000). Short inter-individual distances and/or crowded conditions potentially increase the occurrence of conflicts in both captive and wild primates, and particularly during feeding (Fairbanks and Bird, 1978; Janson and van Schaik, 1988; Mathy and Isbell, 2001; Pruetz and Isbell, 2000; van Schaik, 1989). In some primate species (e.g., rhesus macaque, *Macaca mulatta*; Judge and de Waal, 1997), grooming exchange increases when the number of animals in a restricted area is artificially increased. Moreover, grooming also increases in the minutes before feeding in captive chimpanzees, *Pan troglodytes* (Koyama and Dunbar, 1996), this increase being greater the more is food clumped (Mayagoitia *et al.*, 1993). Finally, grooming is the main affiliative behaviour that primates use to reconcile (reconciliation is defined as "the post-conflict friendly reunion of former opponents that restores their social relationship disturbed by the conflict"; Aureli and de Waal, 2000: p. 387) The function of reconciliation as a tension-reduction mechanism is evident if one considers that the increase of stress-related behaviour observed after a conflict is quickly reduced to baseline levels as soon as reconciliation takes place (Aureli and van Schaik, 1991; Kutsukake and Castles, 2001). The definition of reconciliation explicitly states its function in re-establishing the type of social relationship that former opponents had before the conflict.

b) The importance of grooming in establishing amicable social relationships.

The second hypothesis, now widely accepted, considers grooming essential to the establishment and maintenance of amicable social relationships among group

members (Carpenter, 1942; Oki and Maeda, 1973; Sade, 1972). This is supported by the fact that grooming increases the frequency of reconciled conflicts, cooperative acts, and tolerance near resources, all benefits typically associated with amicable relationships (e.g. Hinde, 1976). For example, immature female blue monkeys tend to exchange grooming with many more group members than males of similar age (Cords, 2000). This pattern may be seen as an attempt by immature females (who are the phylopatric sex in this species) to establish amicable relationships with some other group members. Conversely, long-lasting amicable relationships, and thus grooming exchange, are not particularly important for immature males, who will transfer to new groups once sexually mature. Moreover, Dunbar (1996) found that grooming time increased with group size, presumably because the time needed to service social relationships also increased. Why are amicable social relationships important for group-living primates? All the theories proposed for the evolution of sociality in primates recognise that there are potential costs associated to group living (Dunbar, 1988). These costs are related to the risk of conflict between two or more group members for every limited resource, be it food, grooming or mating partners, play companions, or resting places. Moreover, group-living may favour disease transmission in comparison to solitary life (Nunn *et al.*, 2000). Primates are highly selective in their "choice" of group members with whom to maintain an amicable social relationship, "preferring" close kin as partners. This observation suggests that inclusive fitness or reciprocal altruism (when no close relatives are available; Hamilton, 1964; Trivers, 1971) are at work in the establishment and maintenance of amicable social relationship and thus have to be considered when analysing the benefits of such relationships. One problem here is that grooming and social interactions among group members occur throughout the day, thus making it difficult to prove a cause-effect relation between amicable interactions and their possible benefits (de Waal, 2003). In recent years, however, many studies have presented some evidence on the different benefits that grooming may give to primates.

c) Possible benefits of grooming.

First, grooming may be exchanged for itself due to its hygienic and tension reduction functions (Henzi and Barrett, 1999; Silk *et al.*, 1999; see above). Second, a largely debated benefit of grooming is that it may favour the formation of coalitions. The relationship between grooming exchange between two animals and the likelihood that one of the two will support the other animal in an agonistic contest has been the subject of detailed research (e.g. Harcourt and de Waal, 1992). A positive relationship between grooming and support has been found in many studies (Chapais *et al.*, 1995; Dunbar and Sharman, 1984; Hemelrijk, 1994; Hemelrijk and Ek, 1991; Silk, 1982, Silk *et al.*, 1981) but not in all (e.g. Fairbanks, 1980; Henzi *et al.*, 2003). Third, dyads maintaining stable amicable social relationships through grooming are expected to exchange lower frequencies of agonistic interactions (if one controls for the time that two animals spend in close proximity) and to tolerate each other more than dyads having bad or no social relationships (Hinde, 1976; Kappeler and van Schaik, 1992; Kummer, 1978). For example, tolerance over food is greater the higher the quality (see above) of the relationship between two monkeys (Belisle and Chapais, 2001; Thierry, 2000). Moreover, experimental studies have shown that groomees are more willing to share food with groomers (i.e. animals giving grooming) if a grooming session preceded food provisioning in captive chimpanzees (de Waal, 1989; 1997). A positive relationship also exists between the amount of affiliative interactions between two individuals and the frequency of reconciliation following conflicts (Aureli *et al.*, 1997; Aureli *et al.*, 2002; Castles *et al.*, 1996; Schino *et al.*, 1998). Some authors postulate that a group of females devoting a significant amount of time to grooming and attempting to distribute their grooming about equally to their female companions (see Table 1.1 for a definition of grooming equality), should be particularly cohesive and to co-operate in territory defence when between-group contest food competition is high (Chism and Rogers, 2003; Rowell *et al.*, 1991). To date, however, there is no definitive evidence for a positive relationship between grooming distribution and female participation in inter-group encounters (Cheney, 1981). Fourth, grooming exchange may also favour allo-maternal behaviour. Infant primates are very

attractive for non-lactating females, who often attempt to interact with them (Kohda, 1985). Non-lactating, inexperienced females often are not particularly able to interact with the infants and may in fact represent a potential threat for them (Nicolson, 1987). The benefits of allo-maternal behaviour are still unclear. It has been suggested that allo-mothering may improve the rearing experience of non-lactating females (Lancaster, 1972; Suomi, 1982) and/or reduce the cost of maternal behaviour for lactating females (Nicolson, 1987). Muroyama (1994; see also Henzi and Barrett, 2002) has shown that lactating females are more tolerant towards attempts by females to interact with their infant if those females have previously groomed them. Finally, grooming may also facilitate access to mating partners and information on their reproductive status (Stopka and Macdonald, 1999).

1.4 Grooming Distribution Among Female Primates: Explanatory Models.

The ability to choose the best possible partner is a crucial skill that social primates need to have in order to follow effective social strategies. Indeed, group members have different values as grooming partners, related to their social status or to the number of close relatives or allies in the group. In light of this, different theoretical models have been proposed to predict the distribution of grooming among group members and within grooming bouts. These models may be grouped into two main theories, differing from one another in terms of the importance they give to the various benefits of grooming and to the factors influencing grooming distribution within dyads.

a) Seyfarth's model and its developments.

Around 30 years ago, Seyfarth (1977) proposed an influential model for the distribution of grooming among female primates in relation to their rank, based on the assumption that a cause-effect relationship exists between grooming and coalitionary support. In this model, grooming is predicted to be exchanged more within close kin than between unrelated individuals, as close kin should be more

willing to support one another (due to benefits gained by inclusive fitness). However, dominant females are assumed to be more attractive as grooming partners than lower-ranking females because they could offer more effective coalitionary support. Low-ranking females are, therefore, assumed to compete for grooming access to higher-ranking females. The model thus predicts that grooming would tend to be directed up the hierarchy. Due to competition for access to grooming partners, however, females would spend most of their time grooming individuals with whom they are adjacent in rank. Finally, the interaction between competition for grooming partners and the preference for grooming close kin and high-ranking partners implies a greater cohesiveness (in terms of grooming exchanged) of higher-ranking matrilines.

Sambrook and colleagues (1995) tried to expand the assumptions of Seyfarth model by focusing more on competition for grooming partners than on the importance of grooming for coalitionary support. They predicted that grooming distribution and partner choice is affected by three main factors: 1) rank distance between groomer and groomee, which affects partner attractiveness (de Waal and Luttrell, 1986); 2) engagement of potential partners: the desired grooming partner may already be engaged in grooming with a higher-ranking monkey and thus not be available; 3) interference: a monkey "has learnt" that grooming another individual is likely to result in aggression from, or competition with, other group members and thus inhibits its attempts to access that individual. The authors were, however, unable to present supporting evidence for the importance of these factors in grooming allocation among female baboons (Sambrook *et al.* 1995; Arnold and Whiten, 2003).

Grooming goes up the hierarchy in many primates and it is more frequently given to close-kin and close-ranking individuals (e.g. Coelho *et al.*, 1983; de Waal and Luttrell, 1986; Fairbanks, 1980; Hemelrijk and Ek, 1991; Martel *et al.*, 1994; Sade, 1972), thus supporting Seyfarth's model. Conversely, no convincing evidence is currently available on the relationship between grooming and support (see above). Overall, some studies support the prediction of the model (Seyfarth, 1976; Seyfarth and Cheney, 1984; Vervaecke *et al.*, 2000) while others presents data contrasting it (Coelho *et al.*, 1983; Henzi *et al.*, 2003; Sambrook *et al.*, 1995).

As already noted by Seyfarth (1977), one problem of the model is that active competition for grooming partners is difficult to demonstrate given that the absence of grooming between two individuals may be due to a decision to avoid potential aggression or to a preference for another partner (Henzi *et al.*, 2003). Schino (2001) recently reviewed published data on primate grooming behaviour using meta-analytical techniques in order to test Seyfarth's model. The results of this study provided quantitative support to most of the predictions of the model. However, Schino was not able to test the relation between grooming and agonistic alliance. Moreover, Henzi and Barrett (1999) showed that, despite a general agreement in the literature that coalition formation is common, and grooming and coalitionary support are closely linked, evidence to support this hypothesis are lacking.

b) A model based on the biological market theory.

Seyfarth's model can be considered "static" as it geared only to explain situations in which high ranking females are valuable to low-ranking females (i.e. despotic female-bonded groups) and remains silent on what happens under other conditions. Moreover, it is concerned specifically with the overall pattern of grooming outcome in large primate groups with phylopatric females, strong competition and clear hierarchies (Noë and Hammerstein, 1995). Therefore, it emphasises the effect of rank and kinship on grooming allocation. The recent development of the biological market theory (Noë and Hammerstein, 1995) provides a broader, more dynamic framework to study the distribution of grooming, as it focuses on the process by which these outcomes are generated. This theory aims to explain social strategies in terms of economic laws. In particular, it links the formation of partnerships between animals to trade agreements involving the exchange of valuable commodities (Barrett *et al.*, 1999). Indeed, the basic assumption of the biological market theory is that grooming exchange may give various benefits, including agonistic support (and in this sense, it is a logical extension of Seyfarth's model (Noë and Hammerstein, 1995, p 339)), whose importance may vary among species, habitats, seasons or populations. In contrast with Seyfarth's model, reciprocity, trading and

interchange play a central role in biological market theory, while rank plays only a supporting role. In human markets, goods are exchanged between individuals that differ in their degree of control over those commodities. The preferred traders are those offering the highest value and, hence, competition between traders rises by contest or bidding to be the most attractive partner for the bargain; supply and demand determine the bartering value of commodities exchanged (Noë and Hammerstein, 1995). These rules may also apply to aspects of inter-specific mutualism, such as the exchange of protection for nectar between ants and lycaenid butterfly (Axén *et al.,* 1996; Axén and Pierce, 1998), and the exchange of cleaning for food between cleaner fish and their clients (Bshary, 2001).

Since grooming provides a direct benefit to individuals performing or receiving it (be it parasite removal, tolerance or other), it seems reasonable to consider it as a payoff currency in its own right. The theory postulates that, depending on the goods that are available and that each animal may offer, grooming exchange within a given dyad may range from symmetrical (i.e. the two animals exchange the same amount of grooming and thus grooming reciprocation is high or complete; see Table 1.1) to largely asymmetrical (i.e. one animal gives grooming and the other offers other goods of equivalent value). In other words, individuals may form reciprocal grooming relationships solely for the benefits that grooming itself offers or they may exchange grooming for other goods. In primate groups, where individuals have a range of potential partners from whom to choose, trade should be determined by their standing in the market-place and the goods which they can offer. Depending on the habitat characteristics (e.g. food distribution) and on the resource holding potential (RHP; measured in terms of agonistic power) of the animals, the biological market theory makes the following predictions about grooming distribution and relationships among group members:

1) A given benefit is more expensive to buy the fewer are the individuals that offer it relative to the individuals that demand it (Noë and Hammerstein, 1995).
2) When resources cannot be monopolised, reciprocal traders will spread and dominate in the population since grooming can only be traded for itself.

3) Conversely, when resources are limited and differences in RHP among animals determine access to them, then grooming can be traded for other goods such as support during aggression, tolerance at feeding sites or direct access to the resource itself (de Waal, 1997). Interchange traders are therefore predicted to appear, although reciprocal trading will still be found among individuals with a similar RHP (Barrett *et al.,* 1999). The occurrence of within-group food competition thus makes time matching between grooming given and received be weaker as the rank distance between grooming partners increases. Within the dyads, lower-ranking females are expected to groom their higher-ranking partners more than vice-versa in order to be allowed to gain access to food resources. The trading of grooming for tolerance at feeding sites may thus reduce the overall rank-related difference in feeding success (Saito, 1996).
4) Regardless of the overall aggression rate and level of food competition in a group, an equal amount of grooming exchanged between partners with similar RHP and the immediate reciprocation between non-kin with similar RHP should occur in order to avoid being cheated by grooming partners.

The biological market theory states that the degree of grooming reciprocation within a given dyad depends on the RHP of the animals forming the dyad. Grooming is a time consuming activity (see Section 1.3). Moreover, simultaneous grooming exchange within a dyad (i.e. receiving grooming from, and grooming an animal at the same time) is rare while alternating roles during a grooming session (i.e. one member of the dyad being the groomer first and then the groomee, and vice-versa) is the norm. Therefore, when grooming is exchanged for itself, and thus the degree of grooming reciprocation is expected to be high, an animal might cheat by receiving a large amount of grooming from another individual and then not giving the same amount back. In light of these considerations, the role and the investment in a grooming interaction by each animal depends on the type of social relationship (Section 1.2c) that animal has with its grooming partners. Moreover, they depend on the cognitive ability and capacity to remember past interactions of a species. Two models have been proposed to explain how animals should behave

in order to have a high degree of reciprocated grooming and reducing the risk of being cheated at the same time:

1) The "parcelling model" (Connor, 1995): in this model the groomer and groomee alternate their roles, performing, within each grooming session, a comparable amount of grooming (Hart and Hart, 1992; Mooring and Hart, 1997; Stopka and Graciasová, 2001). Therefore, grooming is immediately reciprocated regardless of the amount of grooming exchanged after each role reversal.
2) The "rise-the-stakes" model (Roberts and Sherratt, 1998): during a grooming session within a given dyad, the partners are expected to keep increasing the duration of reciprocated grooming bouts as the sessions proceed and as interactants gain "trust" in each other. As such, a positive relationship should be found between total duration of a grooming session and length of time that each animal invests in the session as groomer or groomee.

1.5 The Japanese Macaques Living on Yakushima Island, Japan.

The genus *Macaca* is one of the largest within the Primate order and one of the best studied so far (Thierry *et* al., 2004; see Figure 1.2). Yakushima macaques (see Chapter 2 for details on the study site and animals) are an endemic sub-species of Japanese macaque (*Macaca fuscata yakui*), differing from the other sub-species (i.e. *Macaca fuscata fuscata*), living on the main islands of Japan, for their slightly smaller body size and different behavioural ecology (Yamagiwa *et al.*, 1998). Since 1973, Yakushima macaques have been habituated and studied mainly by Japanese researchers (Yamagiwa *et al.*, 1998).

a) Ecology.

The coastal area of Yakushima is covered with a sub-tropical evergreen forest. It is thus largely different from the temperate deciduous forest that is the typical habitat of the Japanese macaques living on the mainland (Yamagiwa *et al.*, 1998).

As a consequence of this, the ecology and social behaviour of Yakushima macaques are different from those of northern populations (Nakagawa, 1998).

The coastal area of Yakushima is a habitat characterised by relatively high quality and abundant food resources (Agetsuma, 1995a). Yakushima macaques are generalist foragers, feeding mainly on fruits, seeds, and leaves in different proportions throughout the year (Agetsuma, 1995a,b; Hanya *et al.*, 2003; Hill, 1997; Maruhashi, 1980). Small animals (mainly insects and spiders), fungi, and other plant parts (e.g. flowers or bark) are also part of the macaques' diet when available. In Yakushima, foraging effort is greatest and time spent moving among food patches least when monkeys are feeding on leaves and when temperatures are low (Agetsuma, 1995a). Population density is higher, home ranges smaller and often largely overlapping with those of neighbouring groups (up to 50% of the area; Maruhashi *et al.*, 1998) in Yakushima than in mainland Japan. Moreover, inter-group encounters are frequent and usually characterised by aggressive interactions (Sugiura *et al.*, 2000). This has led some authors to postulate that inter-group contest food competition is greater in Yakushima than in other parts of Japan (Maruhashi *et al.*, 1998; Sugiura *et al.*, 2000). The rationale for this conclusion is that a given unit of food (e.g. a fruiting tree) is more valuable in Yakushima due to the high population density and thus to the fact that more groups (and animals) may attempt to access or monopolise it. One important consideration here is that most of these comparisons are based on data collected on the Japanese macaque population living on Kinkazan Island, northern Japan, where enough data are available. Kinkazan, however, is considerably smaller than Yakushima (i.e. 10 Km^2 vs. 500 Km^2, respectively) and fewer than 10 groups live there. As such, these comparisons may be related more to the different situations of the two study sites rather than to a different behavioural ecology of the populations.

In any case, the large overlap between neighbouring home ranges (which implies that groups do not actively defend their home range's boundaries) would suggest that competition is more scramble than contest in Yakushima (e.g. Janson and van Schaik, 1988). Moreover, a high level of contest inter-group food competition should in theory favour large groups as they should be more able to

defend food sources than small groups (Wrangham, 1980). In support of the view that inter-group competition for food is more scramble than contest is the observation that the average group size is small in Yakushima (26.6 animals, in comparison to 37.7 animals for groups living on Kinkazan Island; Sprague *et al.*, 1998). Large groups tend to fission when they reach around 50 units (Maruhashi, 1982) while artificially provisioned groups usually fission when the group size exceeds 100 individuals (Koyama, 1970). Group fission, however, may also be due to a high level of intra-group direct food competition (Nakagawa, 1998). Therefore, at the present stage of our knowledge we cannot give a definitive answer on the type of food competition among Yakushima macaques and on its importance for group size.

b) Social behaviour.

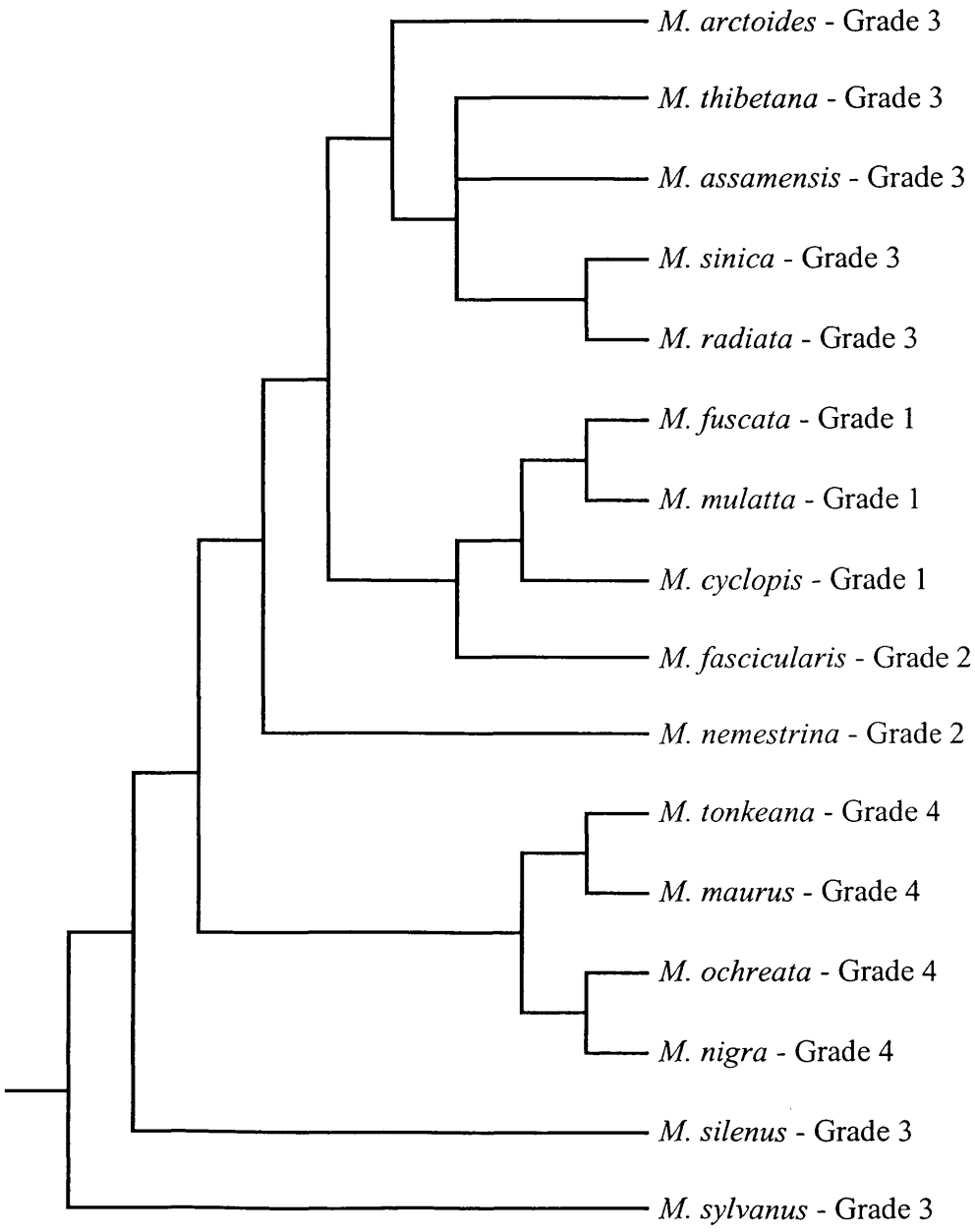
Japanese macaques belong to the Cercopithecidae family (Melnick and Pearl, 1987; see Figure 1.1). Macaque species largely differ in the habitat they inhabit and in the type of social relationships that group members maintain with one another. Thierry (2000; 2004) has attempted to classify this variation in social behaviour and to link it to the phylogenetic relationships among macaque species. He proposed to classify the various species in 4 different grades according to various behavioural characters (see Figure 1.2). These characters mainly relate to the type and intensity of competition between group members, the frequency of reconciled conflicts and the type of grooming distribution. Moreover, they are thought to be an evolutionary consequence of the types of habitat in which macaque species evolved. That is, species characterised by more competitive relationships evolved in habitats where food was clumped and/or scarce and thus where food competition was high, while species with relaxed competitive relationships evolved in areas where direct intra-group food competition was low. In brief, according to Thierry's classification, species belonging to grade 1 show a high frequency of asymmetric conflicts (i.e. conflicts where one monkey is consistently the winner over another monkey), a steep dominance gradient, high grooming preference for kin, low frequency of reconciliation (i.e. 5-20% of total conflicts), low affiliation among unrelated monkeys, and strong rank inheritance

among kin. This grade roughly corresponds to the "despotic" species of another classification of the social style of macaque species (Matsumura, 1996). At the other extreme of the scale, species belonging to grade 4 show a low frequency of asymmetric conflicts, unresolved dominance hierarchies, high frequency of reconciliation (i.e. 40-50% of total conflicts), overall high frequency of grooming among group members and not significantly biased towards kin, and low rank inheritance among kin. Grade 4 is comparable to the egalitarian species of Matsumura's classification (Matsumura, 1996). Species belonging to grades 2 and 3 have social relationships that are intermediate between the two extremes. This classification has to be considered as preliminary, as most of the studies on which it is based have been conducted in captivity (and so they may misrepresent the species-specific social styles; Thierry 2004). This is particularly true for species standing in the middle grades of the scale. The classification, however, is a good starting point for further studies into the behavioural flexibility and diversification of macaque species. With respect to this classification, the Japanese macaque is considered to belong to grade 1 of the scale (see Figure 1.2).

Females are the phylopatric sex in the Japanese macaque and thus usually remain in their natal group and not transfer into new groups. However, when group size decreases dramatically (e.g. N = 1-3 adult females) females have been observed to successfully join larger groups (Sugiura *et al.*, 2002; Takahata *et al.*, 1994). Conversely, males usually leave their natal group when they reach adulthood and may move from one group to another several times during their lifetime (Muroyama *et al.*, 2000; Yoshimi and Takasaki, 2003). Emigration and immigration by males is frequent during the mating season (Sprague, 1991). As temporary visits by males from other groups are frequent during this season, a large number of non-resident males appear around groups, and group fission or takeovers by outside males often occur (Sprague, 1991; Maruhashi, 1982). Immigrant males join a new group at any social status, although the majority of them join at the bottom or top rank (Sprague *et al.*, 1998). When group fission occurs the high-ranking and low-ranking matrilines form two different groups (Maruhashi, 1982). The dominance/subordinance relationship between these two

new groups, however, depends on the dominance/subordinance relationship of the two alpha males (Maruhashi, 1982).

Figure 1.2: Phylogenetic tree of the genus *Macaca* showing the proposed four grades of social style (see text for details) for each species (Purvis 1995; Thierry, 2004).



In Yakushima, the operational sex ratio (OSR; see Table 1.1) is close to 1, and solitary males and all-male groups are rarely found (Sprague, 1992; 1998). Conversely, in provisioned and non-provisioned groups of Japanese macaques in other habitats OSR tends to be much lower than 1 (Yamagiwa and Hill, 1998).

The Japanese macaques show a strict and linear dominance hierarchy (Alexander and Bowers, 1967; Chapais *et al.*, 1991; see above). This means that in this species counterattacks in dyadic confrontations and unresolved dominance/subordinance relationships are rarely observed (Matsumura, 1996). Moreover, percentage of reconciled conflicts is usually lower than approximately 20-30% of total conflicts (Aureli and de Waal, 2000). As a consequence of these observations, Japanese macaques (together with rhesus macaques) are considered to be the most despotic macaque species (Chaffin *et al.*, 1995; Matsumura, 1996; Thierry, 2000; see above). Fully-adult males are usually dominant over females (Melnick and Pearl, 1987). However, females may form coalitions and outrank males, as the two sexes do not differ in size or canine length as much as some other species (e.g orang-utans; Watanabe, 1979).

Females are organised into matrilines composed of closely related individuals (Chapais *et al.*, 1995; Melnick and Pearl, 1987). In this species, dominance relationships between females belonging to the same matriline follow the youngest ascendancy rule (also known as Kawamura's rule; Kawamura, 1958): the youngest daughter of a female ranks immediately below her mother and above all her older sisters (Datta, 1988; Hill and Okayasu, 1996; Koyama, 2003). As a result, females belonging to the same kin group outrank females of other kin groups, and dominance rank among mature sisters is inversely correlated with age. Yakushima macaques seem to not follow Kawamura's rule as the oldest female is usually dominant over her younger sisters. This is probably due to the fact that agonistic support among females is rarely observed in Yakushima and thus youngest daughters do not receive any help from their mothers during agonistic interactions with their older sisters (Hill and Okayasu, 1996). Hill and Okayasu argue that high agonistic support and youngest ascendancy typically occur when resources are concentrated and agonistic interactions over these resources frequent. In this situation, agonistic support by mothers to youngest

daughters (who have high energetic requirements to grow up and reach adult size) is necessary to ensure access to food sources. This conclusion represents additional support for the view that direct food competition is not particularly high in Yakushima (see above).

Confirming former studies on primate social relationships (Hinde, 1976; Kummer, 1978), amicable interactions and coalitions occur with higher frequency among females than among males, given that females are the phylopatric sex in this species and that, unlike males, they often have some related individuals in the group. Indeed, coalitions occur especially among females belonging to the same kin-group (e.g. Nakamichi and Shizawa, 2003), whereas amicable interactions are rarely observed among male Japanese macaques. Macaque males compete for the highest-ranking positions in the group, and high-ranking monkeys aggressively attempt to exclude lower-ranking males from access to oestrus females (Soltis *et al.*, 2001; Takahashi, 2002).

1.6 Aims.

Studying the importance of the different factors affecting grooming distribution in primates, its benefits and costs is important for three main reasons. First, the study of grooming may clarify the strategies that primates follow to establish and maintain amicable social interactions. Second, an analysis of grooming distribution may shed light on the complexity of primate social systems and on the cognitive capacities required for such complexity. Third, from a comparative point of view primate social behaviour may evidence the similarities and differences between human- and non-human societies, and help us to understand the social organisation of primitive and modern human societies. Hence, the study of grooming may have important implications for evolutionary and social psychology, social or cultural anthropology and ethnology (Dunbar, 1998). Notwithstanding this, the importance of the proximate and ultimate factors affecting grooming distribution in primate societies is still unclear. Moreover, there is no general agreement on the benefits of grooming exchange. It is

particularly interesting to study this topic in the sub-species of the Japanese macaque living on Yakushima Island (*Macaca fuscata yakui*), given its particular behavioural ecology (see Section 1.5). Therefore, the aims of this Thesis were:

1) To analyse the effect of abiotic factors (i.e. time of day, ambient temperature, and relative humidity) on time spent grooming or on other behaviours that are related to the care of the pelage (i.e. self-grooming or self-scratching, hereafter scratching; Chapter 3);
2) To compare two methodological approaches (based on dyads and on matrices, respectively) to the analysis of grooming distribution and reciprocation, and to discuss their efficacy and reliability (Chapter 4);
3) To analyse how grooming distribution and reciprocation are affected by seasonal variations in activity budgets, diet composition and food abundance (Chapter 5);
4) To determine how group size affects grooming distribution and reciprocation (Chapter 6);
5) To analyse the possible benefits of grooming exchange and to discuss the social tactics that primates follow to maximise their fitness (Chapter 7);
6) To provide an overall synthesis of the findings of this study and discuss their potential implications for our comprehension of primate social relationships and human social behaviour (Chapter 8).

Table 1.1: Definitions of some terms used in this Thesis (see Table 2.4 for definitions of the behavioural categories analysed in this study).

Term	Definition
Fitness	The reproductive success of an animal, measured as the number of offspring produced throughout its life or as the number of offspring produced who reached reproductive age (Ridley, 1996).
Inclusive fitness	The reproductive success of an animal (i.e. fitness) plus that of its relatives (Hamilton, 1964). It follows that, other things being equal, the inclusive fitness of an animal will increase more when its close relatives produce offspring than when its distant relatives do the same.
Altruism	An altruistic act between two animals is defined as a behaviour that increases the fitness of the receiver and inflicts some costs to the donor (Ridley, 1996).
Reciprocal altruism	Two animals exchanging altruistic acts in order to balance the benefits and costs of these acts. To avoid cheating, reciprocal altruistic acts between two animals may occur simultaneously or sequentially (Trivers, 1971).
Kin selection	The evolutionary force working on closely-related animals: an animal is expected to bias its altruistic acts towards relatives in order to increase its inclusive fitness.
Foraging efficiency	How much food an animal is able to get in a given amount of time. Foraging efficiency thus depends on the abundance and spatial distribution of resources, on how much work has to be done to find or get the food (e.g. nuts with hard shells or animals), on the level of food competition, on the energetic content and digestibility of food.
Operational sex ratio	The ratio between the number of males and females in a group who are reproductively active. OSR is thus different from the socionomic sex ratio which in the ratio between

	the total number of males and females in a group, regardless of reproductive status. Macaque groups often have a OSR ranging between 0.4 and 0.7 (Melnick and Pearl, 1987).
Grooming reciprocation	A grooming interaction between two individuals is highly reciprocated if the amount of grooming that each animal gives to, and receives from the other is closely matched. To study the degree of reciprocation some authors (Barrett *et al.*, 1999, 2000) use immediately reciprocated grooming bouts (i.e. the amount of grooming that one animal gives to, and immediately after receives from the same animal). Other authors (Schino *et al.*, 2003) use the total amount of grooming exchanged between two animals during a grooming session (which may involve the animal giving to, and receiving grooming from the same animal at different points within the session) or during the course of the study. See the rest of the Thesis and in particular Chapter 4 for an extensive discussion on grooming reciprocation.
Grooming equality	A measure of how each animal distributes its grooming among the various group members. In this thesis, grooming equality is measured through the Shannon-Wiener diversity index (see Chapter 5 for more details on the index). I define as the ideal grooming equality for a given monkey when the animal grooms all its group companions for the same amount of time, regardless of the total amount of time the animal devotes to grooming. At the other extreme, grooming is completely unequally distributed when an animal grooms only one group companion and ignores the others, or it does not groom any animal at all.

CHAPTER 2

GENERAL METHODS

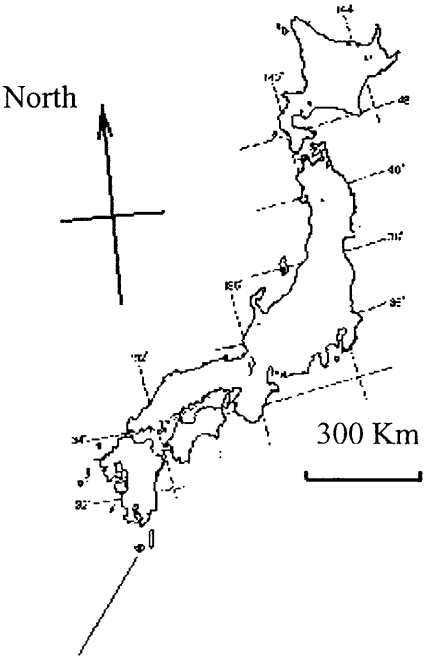
2.1 Study Area and Subjects.

a) Study area.

Yakushima is a volcanic island of around 500 km^2 located 60 km south of Kyushu, Japan (31°N, 131°E; Figure 2.1). The Island is covered with a sub-tropical evergreen forest on the coast, approximately up to 500 m above sea level, and with a deciduous forest on the mountains. The highest peak of the island is 1,935 m a.s.l. The coastal forest is part of the Kirishima-Yaku National Park that covers most of the mountains of the island. The study area is in the western slope of the island between the coast and around 400m a.s.l. Although a road crosses the area, human activities (e.g. logging, presence of tourists) and food provisioning of macaques are prohibited. This contrasts with most of the long-studied populations of Japanese macaques that are often provisioned and/or live near human settlements. As such, Yakushima represents one of the few field sites in Japan where ranging patterns and social behaviour of the Japanese macaques are scarcely affected by human presence.

Distylium racemosus, *Ficus superba*, *Ficus microcarpa, Camelia japonica*, and *Ardisia sieboldii* are the dominant tree species on the coastal forest (Yamagiwa *et al.*, 1998). Temperature ranges from a minimum of about 3°C to a maximum of about 32°C, average rainfall is between 100 and 400 mm each month but it is higher than 400 mm in June, which is the peak of the rainy season (Hill, 1997). Japanese macaques and sika deer (*Cervus nippon yakushimae*) are the only large mammals living on the island and no predators of the Japanese macaques are present (Agetsuma *et al.*, 2003).

Figure 2.1: Map of Japan; Yakushima Island is enlarged and the approximate position of the study area is indicated.



Yakushima Island enlarged

a) Study subjects.

Subjects of this study were two non-neighbouring groups of Japanese macaques living in two valleys around 1 Km apart. One group (Nina A) was previously studied by other researchers (e.g. Soltis *et al.*, 2000) and was thus well habituated to human presence. Moreover, the monkeys were habituated to my presence during May and June 2001. Habituation of a group to human presence was achieved by trying to spend as much time as possible with the monkeys while avoiding any sudden movement. After a couple of weeks the monkeys started to appear less disturbed by my presence as they did not give any alarm call and did not run away when I was trying to approach them. In June, monkeys could be approached within 5 metres without any apparent effect on their behaviour and the individual I.D. of the monkeys was thus possible.

At the beginning of the study (May 2001) Nina A group consisted of 21 sub-adult/adult monkeys (age ≥ 4 years; 13 males and 8 females), 3 yearlings, and 1 infant. Kw group was first habituated by Mr. Hiroki Koda during August / October 2001 and then by Dr. Bonaventura Majolo and myself during November and December 2001. At the beginning of the study (January 2002) this group consisted of 22 sub-adult/adult females, around 15 sub-adult/adult males, 3 infants and an indefinite number of yearlings and juveniles. The estimated group size for Kw group was around 55-60 monkeys.

For this thesis, data were collected on all the monkeys ≥ 4 years old, living in Nina A group (N = 21) and on the 22 sub-adult/adult females living in Kw group (Table 2.1 to 2.3 for details on the study animals). Age of Nina A females was known from the back-records available at the Yakushima Field Station of Kyoto University. For Kw females, age was estimated by size and sexual activity during the previous mating season. Size, sexual swelling or capacity to ejaculate was used to estimate age of Nina A males and Kw females. Seven males living in Nina A group emigrated to other groups during October 2001 but they were included in the statistical analyses (Chapter 3). No monkey died or disappeared in Nina A group during the course of the study. However, 2 adult females living in Kw group disappeared: one in December 2001 (during the habituation period) and the other female after 7 days from the beginning of the data collection. These females

were excluded from all the statistical analyses and thus the sample size for Kw females was reduced to 20 females. All the monkeys who were part of the data collection were individually recognised by the observers.

Table 2.1: Details of Nina A females (N = 8; data collected from June 2001 to May 2002).

Monkey	Hrs of focal data / Hrs from Jan to May 2002 (see text for details)	Rank
Syako	18.4 / 8.9	1
Shijimi	17.5 / 8.8	2
Hanabi	18.8 / 8.1	3
Yamaimo	18.4 / 9.3	4
Yamayuri	18.7 / 8.4	5
Ramu	18.3 / 8.0	6
Hotate	18.3 / 8.9	7
Hotaru	17.5 / 8.7	8

Table 2.2: Details of Kw females (N = 20; data collected from January to May 2002).

Monkey	Hrs of focal data	Rank
Zina	7.4	1
June	7.3	2
Livia	7.7	3
Doris	7.7	4
Zazie	7.3	5
Blanche	6.9	6
Hannah	6.4	7
Nobuko	7.1	8
Fumiko	7.5	9
Miyo	6.5	10
Chichi	4.1	11
Chocolat	7.1	12
Anie	7.5	13
Kiki	7.0	14
Anne	7.1	15

Olive	6.9	16
Sara	7.3	17
Raffi	7.0	18
Eli	7.0	19
Eliza	7.1	20

Table 2.3: Details of Nina A males (N = 13; * males who left the group during the course of the study; data collected from June 2001 to May 2002).

Monkey	Hrs of focal data	Rank
Shark	14.4	1
India	16.0	2
Momo *	7.9	3
Babe	11.8	4
Syachihoko *	7.2	5
Jacknife	12.8	6
Shishi *	6.3	6
Noritama	11.9	8

Roku	13.0	9
Byakko *	5.9	10
Rakko *	7.3	11
Josif *	6.1	12
Bino *	8.5	13

2.1 Data Collection.

The data used in this thesis were collected by two observers: Dr. Bonaventura Majolo and myself. The data collection began when inter-observer agreement was over 95%. In order to avoid repetition, Chapters 3 to 7 will only contain specific details of the methodology used in each chapter and will not be given here.

Data on Nina A group were collected from the 22nd June 2001 to the 4th May 2002 whereas data on Kw females were collected from the 24th January to the 4th May 2002. During the study, there were only two gaps in the data collection: from the 2nd to the 10th of September 2001, and from December 20th 2001 to January 23rd 2002.

Data were collected following three different sampling methods (i.e. *ad libitum*, scan, and focal sampling) and two sampling rules (i.e. instantaneous, all occurrences; Altmann, 1974; Martin and Bateson, 1993). Data were collected *ad libitum* on behaviours that occurred rarely, such as agonistic interactions. Scan sampling (using instantaneous sampling) was used to obtain activity budgets as this sampling method, in comparison to focal sampling, reduces the chances of concentrating observations on monkeys displaying more conspicuous behaviour. Focal sampling (using all occurrences sampling) was, however, used to obtain durations and frequencies of social interactions between the study animals. Data

were collected on various social behaviours (friendly or agonistic) to obtain information about the type of social relationships that each monkey had with its group companions, and on behaviours used for the care of the pelage (i.e. self-grooming and scratching). All behaviours recorded in this study are defined in Table 2.4. The identity of all individuals involved in behavioural interactions was recorded when possible.

Table 2.4: Definitions of the behavioural categories recorded (S: behavioural state; E: behavioural event; see Martin & Bateson, 1993 for definitions. * Data collected only during focal-sampling sessions; aggressive behaviour was also recorded *ad libitum*).

Behaviour	Definition
Giving grooming (S)	The focal animal carefully picks through and/or slow brushes aside the fur of another individual with one or both forepaws. The material that is picked out, such as small hairs and flakes of skin, may be placed into the mouth (Rosenblum *et al.*, 1966). A grooming bout is considered as the time the groomer spends grooming another individual, not interrupted by pauses longer than 30 seconds (Schino *et al.*, 2003).
Receiving grooming (S)	The focal animal receives grooming (see above for definition) from another individual and this activity is not interrupted by pauses longer than 30 seconds.
Self-grooming (S)	The focal animal grooms itself (see above for definition) and this activity is not interrupted by pauses longer than 30 seconds.

Grooming solicitation (E) *	The focal animal approaches, or is approached by, another individual, presenting the back of its body to it in order to receive grooming. The focal animal may give or receive this behaviour. A grooming solicitation was considered to be successful if within 10 seconds a grooming interaction began between the two animals.
Displacement groomer / groomee (E) *	The focal animal interrupts a grooming interaction between two other individuals substituting the groomer or the groomee. The individual substituted is subordinate to the focal animal. The focal animal may give or receive this behaviour.
Proximity (S) *	The focal animal is ≤ 1 metre from one or more individuals.
Approach (E) *	The distance between the focal animal and one or more individuals is reduced from > 1 metre to ≤ 1 metre. The actor of this behaviour is considered the animal that actively reduce its distance from one or more individuals.

Aggressive behaviour (E) *	This category includes threat (the monkey opens its mouth without showing its teeth, flaps its ears, stares at its opponent, or slaps its hand on the ground), chase, and physical assault (the monkey attacks another animal, biting, grabbing, or slapping it) towards another individual. The focal animal may give or receive an aggressive act. An aggressive behaviour was considered to be food-related when one or all the opponents were foraging (i.e. chewing, searching for food or picking up food items).
Submissive behaviour (E) *	The focal animal flees when approached by another individual or directs a "bared-teeth display" to it (de Waal and Luttrell, 1986). The focal animal may give or receive an aggressive act.
Scratching (E) *	The focal animal repeatedly and rapidly moves its hand or foot drawing its fingertips across its own fur (Schino *et al.*, 1988)

a) Dominance/subordinance relationships and aggressive behaviour.

Data on the dominance/subordinance relationships among the study animals were recorded *ad libitum* every time one monkey was observed to avoid or was displaced by another monkey in a non-agonistic context. Moreover, data on conflicts between two monkeys, not involving third parties, and with a clear-cut result (i.e. decided: one of the opponents showed clear signs of submission) were used for the same purpose. The hierarchical status of the monkeys was analysed separately for Nina A males and females. All the agonistic interactions observed were entered into matrices (see Tables 2.5 to 2.7) and analysed using Mat Man 1.0 to assigned a hierarchical rank to each animal. The value 1 was given to the

highest-ranking male/female, 2 to the beta individual, and so on to the following monkeys. The percentage of agonistic interactions with a clear-cut result for Nina A females was 99.5% and it was 100% for both Kw female and Nina A males. No monkey changed its relative rank during the course of the study. Nina A males who remained in the group simply improved their absolute social rank according to the number of males who had left the group (see Section 2.1b) and who had ranked above them. The frequency of aggressive interactions per individual or dyad was obtained from focal data (see below), by dividing the number of aggressive acts per the total hrs of data collected on each individual or dyad.

b) Grooming exchange.

Scan sampling was used to determine the amount of time that each study animal spent grooming. Every hour the activity (i.e. grooming vs. other: foraging, moving, resting or sexual behaviour; see Table 2.4) of all the animals, who were visible within one minute from the beginning of the scan, was recorded using instantaneous sampling. For each monkey, data on time spent grooming were transformed into percentages of time spent displaying each behaviour using the formula:

(N of scans in which the animal was involved in a grooming interaction / Total N of scans for each animal) x 100

Focal animal sampling was used to record social interactions (i.e. aggressive or submissive behaviour, giving or receiving grooming, grooming solicitation and displacement groomer/groomee; see Table 2.4) among the study animals, self-grooming or scratching. Observation sessions lasted 10 minutes and between 3 and 6 sessions per week were collected on each monkey. The duration of the focal observations was established during a pilot study conducted in May 2001. This pilot study demonstrated that focal sessions lasting more than 10 minutes often had to be interrupted due to the focal animal running away or disappearing in the canopy. This was due to the steepness of the area and to the frequent changes of activity by the monkeys. Observation sessions were distributed approximately equally from 8.00 to 19.00 for each monkey (see Table 2.1 to 2.3 for the amount of hours collected on each study animal). All occurrences sampling was used to

obtain the frequency of behavioural events (i.e. events / hr; see Table 2.4) and the duration of behavioural states. For each monkey, behavioural states were then transformed into percentages of time spent displaying each behaviour following the formula:

(Total minutes for each behaviour / Total minutes collected on each monkey) x 100

When the focal animal could not be followed for the whole duration of the session, all the observation sessions lasting 6 minutes or more were retained while the others were discarded.

Throughout the thesis I defined a "non-reciprocal grooming bout" *sensu* Barrett *et al.* (1999), as when the groomer stops grooming her partner but she does not then receive grooming from her partner immediately. On the contrary, I designated as a "reciprocal grooming bout" when I observed two consecutive grooming episodes in which female 1 grooms female 2 and then as soon as female 1 stops, female 2 commences grooming.

Table 2.5: Dominance matrix for Nina A females (N = 8) showing the number of aggressive interactions with a clear-cut result per dyad.

Winner	Loser							
	Syako	Shijimi	Hanabi	Yamaimo	Yamayuri	Ramu	Hotate	Hotaru
Syako		1	7	24	11	9	7	13
Shijimi			14	19	15	1	1	8
Hanabi				25	25	22	15	17
Yamaimo					32	12	13	22
Yamayuri						17	6	13
Ramu							1	25
Hotate								17
Hotaru								

Table 2.6: Dominance matrix for Kw females (N = 20) showing the number of aggressive interactions with a clear-cut result per dyad (the Table continues on the next page).

Winner	Loser																				
	Zina	June	Livia	Doris	Zazie	Blanche	Hannah	Nobuko	Fumiko	Mijo	Chichi	Sara	Anie	Kiki	Anne	Olive	Chocolat	Raffi	Eliza	Eli
Zina		1	5	2	1	1		1	3		2	3	6	2	1	3	1	2	1	1
June			1	6	9	1	1	2		1		4	8	1	1	1	5	2	2	3
Livia				1	7	1	2	2				3	6	1			3	2	1	
Doris					8	1		4	2	4			2	4	3	1	4	4		1
Zazie							8	2	1	3	1	7	3	3	3		5	4		2
Blanche							4		1	1	1		3	2	1		3	3		
Hannah									3	1		1	1		1	1		2		2
Nobuko									3			2	2	4		1				
Fumiko												1	7	3	1	3	2	1	2	1
Mijo													1					3		2
Chichi												1								
Sara																	1	1	4	7
Anie														2	2	3				2

Table 2.6: Dominance matrix for Kw females (N = 20) continued.

Winner	Loser																			
	Zina	June	Livia	Doris	Zazie	Blanche	Hannah	Nobuko	Fumiko	Mijo	Chichi	Sara	Anie	Kiki	Anne	Olive	Chocolat	Raffi	Eliza	Eli
Kiki															5	7				
Anne																1	1	1		
Olive																	1			2
Chocolat																			2	6
Raffi																			1	2
Eliza																				
Eli																				

Table 2.7: Dominance matrix for Nina A males (N = 13) showing the number of aggressive interactions with a clear-cut result per dyad.

Winner	Loser												
	Shark	India	Momo	Syachihoko	Babe	Jacknife	Shishi	Noritama	Roku	Byakko	Josif	Rakko	Bino
Shark		56	14	9	22	18	21	15	44	9	1	4	2
India			5	4	12	6	8	8	21	2	2	1	3
Momo				1	7	4				1	4		2
Syachihoko						2	8	2	1	2		3	
Babe						23	3	4	16				2
Jacknife								2	32			1	6
Shishi										1	2	4	
Noritama									11			1	2
Roku										1	1		9
Byakko											5	6	1
Josif													5
Rakko													
Bino													

2.3 Data Analysis.

In this thesis data were analysed using non-parametric statistics (Everitt, 1996; Howell, 1999; Siegel and Castellan, 1988) or matrices. However, parametric statistics was used when no comparable non-parametric test was available (see Chapter 3). All the tests were two-tailed and significance was set at $p < 0.05$. The particular statistical tests used in this thesis will be discussed in the methods section of each of the following chapters.

CHAPTER 3

DIFFERENTIAL EFFECTS OF AMBIENT TEMPERATURE AND HUMIDITY ON GROOMING, SELF-GROOMING, AND SCRATCHING

This chapter aims to determine the effect of abiotic factors on the occurrence of grooming, self-grooming and scratching. Subjects of this study (see Chapter 2 for details) were all the sub-adult/adult monkeys (i.e. age ≥ 4 years) living in Nina A group (N = 21; 8 females and 13 males).

3.1 Introduction.

A number of studies have investigated the effects of climatic variations on the behaviour and time budget of primates (e.g. black and gold howler monkey, *Alouatta caraja*: Bicca-Marques and Calegaro-Marques, 1998; western black and white colobus, *Colobus polykomos*: Dasilva, 1993; chacma baboons, *Papio cynocephalus ursinus*: Hill *et al.*, 2004; gelada baboons, *Theropithecus gelada*: Iwamoto and Dunbar, 1983; ruffed lemurs, *Varecia variegata variegata*: Morland, 1993; redfronted lemurs, *Eulemur fulvus rufus*: Ostner, 2002; yellow baboons, *Papio cynocephalus cynocephalus*: Pochron, 2000; Stelzner, 1988; common marmosets, *Callithrix jacchus*: Suchi and Rothe, 1999). All these studies have found a similar and persistent pattern: animals tend to be less active at the extreme ranges of ambient temperature or when relative humidity is particularly high. However, the strength of these effects differs in different species, as it depends on the breath of the climatic variation of the habitat.

Variations in temperature and humidity have the potential to force an animal to adjust its time budget and, ultimately, even to give up time devoted to specific activities such as social time (Conradt *et al.*, 2000). For example, because thermoregulation is affected by body contact between individuals, monkeys tend to engage in more inter-individual contact under condition of lower ambient

temperatures and thus to devote less time to other activities (e.g. moving; Brent *et al.*, 2003; Dahl and Smith, 1985; Dahl *et al.*, 1986; Schino and Troisi, 1990, 1998).

Grooming, the main behaviour servicing primate social relationships (see Chapter 1), presents a more confused picture. Although earlier studies identified a possible relation between the amount of time monkeys spent grooming and variations in climatic conditions (i.e. more grooming was observed in the hottest hours of the day), they provided little or no statistical analyses and are therefore difficult to interpret (e.g., Bernstein and Mason, 1963; Bernstein, 1972; Bernstein, 1980). Quantitative assessments of the influence of ambient temperature and relative humidity on grooming have been presented by only a few studies. Hill and colleagues (2004) found an inverse relation between grooming and both temperature in shade and humidity in wild chacma baboons. Troisi and colleagues (1982), studying captive Japanese macaques (*Macaca fuscata*), reported that the occurrence of grooming was not affected by climatic variations (temperature range: 1-31 °C; humidity range 34-100 %), while Troisi and Schino (1986, in captive long-tailed macaques, *M. fascicularis*) observed more grooming under conditions of higher temperature and lower relative humidity (temperature range: 12-37 °C; humidity range 25-89 %). In long-tailed macaques grooming is not the only behaviour that is influenced by climatic variations. Self-grooming and scratching show similar susceptibility to environmental influences (Troisi and Schino, 1987; Pavani *et al.*, 1991), suggesting that in this species all behaviours related to the maintenance of the pelage may be similarly affected by variations in ambient temperature and humidity.

Based on the contrast that had been observed in the effects of ambient temperature and humidity on the grooming behaviour of Japanese and long-tailed macaques, Troisi and Schino (1986) speculated that the adaptation of the Japanese macaques to the temperate climate of Japan may have required its grooming to be unaffected by variations in ambient temperature and humidity in order not to jeopardise its social function under the relatively harsh climatic conditions. In other words, if grooming was affected by climatic variations then Northern populations of Japanese macaques (facing temperatures close or below zero

Celsius degrees for 5-6 months per year) would have too little time available for grooming to be able to maintain cohesive and amicable relationships with their group companions. As a consequence of this, the invasion into cold climates by ancestral macaques favoured the progressive independence of grooming from climatic conditions.

The aims of this study were to provide quantitative data on the influence of ambient temperature and humidity on the occurrence of behaviours related to the maintenance of the pelage (i.e. grooming, self-grooming and scratching) in Nina A group. Variations in females' and males' responses to climatic factors were also investigated. Moreover, this study aimed to discuss the results in light of the functional contrast that exists between grooming, which has both social and hygienic functions, and self-grooming and scratching, which have solely hygienic functions (Barton, 1985; Muroyama, 1991; Tanaka and Takefushi, 1993).

3.2 Methods.

a) Study subjects and weather conditions.

Subjects of this study were all the sub-adult/adult monkeys (i.e age $\geq$ 4 years) living in Nina A group (i.e. N = 8 females and N = 13 males; see Chapter 2 for details of the study animals). During the study period, temperatures ranged from 8°C to 34°C, and relative humidity from 26 % to 96 %.

b) Data collection.

Data were collected from June 2001 to May 2002 on Nina A monkeys (see Chapter 2 for definitions). Data presented here come from a total of 362.6 hrs of focal animal sampling (207.3 hrs for females and 155.3 hrs for males), ranging from 5.9 hrs to 26.9 hrs per individual. During the course of the study, female monkeys spent on average 39.5 % ± 1.0 % (mean ± SE) of their time grooming and 2.4 % ± 0.1 % (mean ± SE) self-grooming. Male monkeys spent on average 33.0 % ± 1.2 % (mean ± SE) of their time grooming and 3.4 % ± 0.2 % (mean ±

SE) self-grooming. Overall frequency of scratching was 18.0 ± 0.51 for females and 23.8 ± 0.77 for males (mean events per hr ± SE).

Temperature and relative humidity were recorded by an electronic thermometer-hygrometer each time a focal session began, at about 1 m from the ground. Simple temperature indices represent a useful proxy of the thermal characteristics of a monkey's "perceived" environment (Hill *et al.*, 2004).

c) Data analysis.

Grooming and self-grooming were expressed as percentages of time spent in each of the two behaviours, scratching as the frequency of scratching per hour of observation (rate), (see Chapter 2). Data entered into analyses were individual scores for each observation session (N = 1203 for females; N = 910 for males). Statistical tests were run three times: for the whole sample subjects, for females and for males independently, in order to investigate sex differences in the relation between grooming / scratching and ambient temperature / humidity. Since each subject was sampled repeatedly and since significant interindividual differences in the overall frequency of the behaviours recorded during the study existed, the effects of ambient temperature and humidity could not be tested by simple regressions (Everitt, 1996). Instead, I used analyses of covariance (ANCOVA) in which individual identity was inserted as a categorical factor and ambient temperature (or humidity) as a regressor. The main effect of temperature (or humidity) tests for the existence of a significant relation between temperature (or humidity) and behaviour while controlling for interindividual variation and avoiding pseudoreplication. The interaction effect between temperature (or humidity) and individual identity tests whether the effect of temperature (or humidity) is the same in all subjects (test of the homogeneity of slopes). Although the data were not normally distributed, I used parametric ANCOVAs because they are relatively robust to violations of the assumption of normality (Everitt, 1996), and no equivalent non-parametric test is currently available (Siegel and Castellan, 1988). The p values reported are therefore to be interpreted with caution. In order to confirm the results with a non-parametric technique the data were split in two groups, each approximately with the same range of temperature (the same

criterion was used for humidity; see below): those recorded under conditions of lower temperatures (8-21 °C) and those recorded under conditions of higher temperatures (22-34 °C). Individual averages were calculated for the two of temperature conditions and compared using the Wilcoxon matched pairs test. Subjects that had been observed for less than 1 h under either condition of temperature were discarded from analysis. The same procedure was used to confirm the effects of relative humidity (lower: 26-61 %; higher: 62-96 %).

Time of day is a potentially confounding variable, since marked variations in both activity patterns and temperature and humidity exist (see also Clutton-Brock and Harvey, 1977; Hill *et al.*, 2004). Its effect on macaque behaviour was assessed by one-way ANOVAs.

For grooming, I present only the results on the time each individual spent actively grooming a partner. Analyses run on the total time each individual spent grooming (i.e., time spent grooming plus time spent receiving grooming) gave, however, the same results. Since too little data were recorded between 7.00 and 8.00 hrs and between 17.00 and 18.00 hrs, I collapsed sessions recorded between 7.00 and 9.00 hrs as well as those between 16.00 and 18.00 hrs.

3.3 Results.

a) Grooming.

Japanese macaques spent similar amounts of time grooming in the different hours of the day (all subjects: females: $F = 0.371$, $df = 8/2016$, NS; $F = 0.890$, $df = 8/1203$, NS; males: $F = 1.034$, $df = 8/910$, NS).

Ambient temperature exerted no overall effect on the time spent grooming by the group as a whole, and individual identity had no significant effect (Table 3.1). However, ambient temperature exerted an overall effect on the time spent grooming by the females, and this effect varied among the different individuals (Table 3.2). On the contrary, male grooming was not influenced by temperature (Table 3.3). The mating season is known to affect the grooming behaviour of Japanese macaques as the overall proportion of time spent grooming decreases

and females tend to groom adult males rather than females (D'Amato *et al.*, 1982). Moreover, since ambient temperature also differs in the different seasons, I analysed separately the data collected in the mating and the non-mating seasons (see Chapter 1 for a criterion to define the mating season). Effects of temperature were again non-significant considering all Nina A group members (Table 3.1). The effect of temperature was confirmed to be significant for females in the mating season (Table 3.2) but individual identity did not have a significant effect. However, temperature did not influence female grooming behaviour during the non-mating season (Table 3.2), even though individuals responded differently to this climatic factor. Male grooming was not affected by temperature during either the mating or the non-mating season (Table 3.3). All male individuals showed similar patterns of behaviour when temperature varied in the two periods (Table 3.3). Finally, a Wilcoxon test comparing grooming under conditions of lower (8-21°C) and higher (22-34°C) temperatures indicated no effect of ambient temperature on grooming for the whole group ($T = 27$, $N = 15$, NS) or for either sex (females: $T = 25$, $N = 8$, NS; males: $T = 16.5$, $N = 7$, NS; Figure 3.1).

Relative humidity did not influence time spent grooming by all Nina A subjects, and the influence did not vary among the different individuals (Table 3.1). A similar trend emerged analysing the two sex classes separately (Table 3.2 for females and Table 3.3 for males, respectively). Again, analyses for the mating and the non mating season yielded similar results for the whole group (Table 3.1) and in females (Table 3.2), if one excludes the significant Humidity x Individual identity interaction in the non-mating seasons. Independent analyses for the mating and the non-mating season produced non-significant results in males too (Table 3.3). Finally, grooming recorded under conditions of lower (26-61 %) and higher (62-96 %) humidity did not differ significantly in the whole group ($T = 52$, $N = 14$, NS) or in both the sexes (females: $T = 29$, $N = 8$, NS; males: $T = 12$, $N = 6$, NS; Figure 3.2).

Table 3.1: The effect of ambient temperature and relative humidity on grooming for all Nina A group members (N = 21; * $p < 0.05$).

Climatic factor	Study period	Effect	F value, d.f and significance
Temperature			
	Overall		
		Temperature	0.71 (1/2073), NS
		Individual identity	1.10 (20/2073), NS
		Temperature x Individual identity	1.21 (20/2073), NS
	Mating season		
		Temperature	0.70 (1/975), NS
		Individual identity	0.81 (20/975), NS
		Temperature x Individual identity	0.91 (20/975), NS
	Non-mating season		
		Temperature	1.10 (1/1056), NS
		Individual identity	1.16 (20/1056), NS
		Temperature x Individual identity	1.32 (20/1056), NS
Humidity			

Overall		
	Humidity	0.38 (1/2073), NS
	Individual identity	1.61 (20/2073), *
	Humidity x Individual identity	1.45 (20/2073), NS
Mating season		
	Humidity	1.59 (1/975), NS
	Individual identity	0.99 (20/975), NS
	Humidity x Individual identity	0.64 (20/975), NS
Non-mating season		
	Humidity	0.00 (1/1056), NS
	Individual identity	1.44 (20/1056), NS
	Humidity x Individual identity	1.49 (20/1056), NS

Table 3.2: The effect of ambient temperature and relative humidity on grooming for Nina A females (N = 8; * $p < 0.05$; ** $p < 0.01$).

Climatic factor	Study period	Effect	F value, d.f and significance
Temperature			
	Overall		
		Temperature	6.26 (1/1203) *
		Individual identity	1.96 (7/1203), NS
		Temperature x Individual identity	2.54 (7/1203) *
	Mating season		
		Temperature	5.30 (1/554) *
		Individual identity	0.70 (7/554), NS
		Temperature x Individual identity	0.64 (7/554), NS
	Non-mating season		
		Temperature	1.30 (1/648), NS
		Individual identity	2.15 (7/648) *
		Temperature x Individual identity	2.87 (7/648) **
Humidity			

Overall		
	Humidity	0.02 (1/1203), NS
	Individual identity	2.32 (7/1203) *
	Humidity x Individual identity	2.36 (7/1203), NS
Mating season		
	Humidity	2.08 (1/554), NS
	Individual identity	1.11 (7/554), NS
	Humidity x Individual identity	0.61 (7/554), NS
Non-mating season		
	Humidity	0.39 (1/648), NS
	Individual identity	2.42 (7/648) *
	Humidity x Individual identity	3.09 (7/648), NS

Table 3.3: The effect of ambient temperature and relative humidity on grooming for Nina A males (N = 13).

Climatic factor	Study period	Effect	F value, d.f and significance
Temperature			
	Overall		
		Temperature	0.06 (1/910), NS
		Individual identity	0.57 (12/910), NS
		Temperature x Individual identity	0.45 (12/910), NS
	Mating season		
		Temperature	0.02 (1/461), NS
		Individual identity	1.03 (12/461), NS
		Temperature x Individual identity	1.25 (12/461), NS
	Non-mating season		
		Temperature	1.37 (12/448), NS
		Individual identity	0.66 (12/448), NS
		Temperature x Individual identity	0.56 (12/448), NS
Humidity			

	Overall		
		Humidity	0.48 (1/910), NS
		Individual identity	1.34 (12/910), NS
		Humidity x Individual identity	0.88 (12/910), NS
	Mating season		
		Humidity	0.58 (1/461), NS
		Individual identity	0.88 (12/461), NS
		Humidity x Individual identity	0.80 (12/461), NS
	Non-mating season		
		Humidity	0.00 (1/448), NS
		Individual identity	0.95 (12/448), NS
		Humidity x Individual identity	0.61 (12/448), NS

Figure 3.1: Percentage of time spent grooming by the study animals under condition of lower (8-21°C) and higher (22-34°C) ambient temperature (means ± SE).

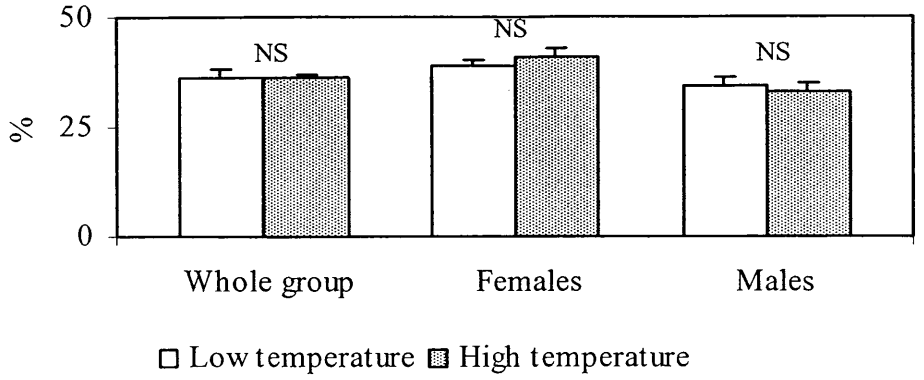
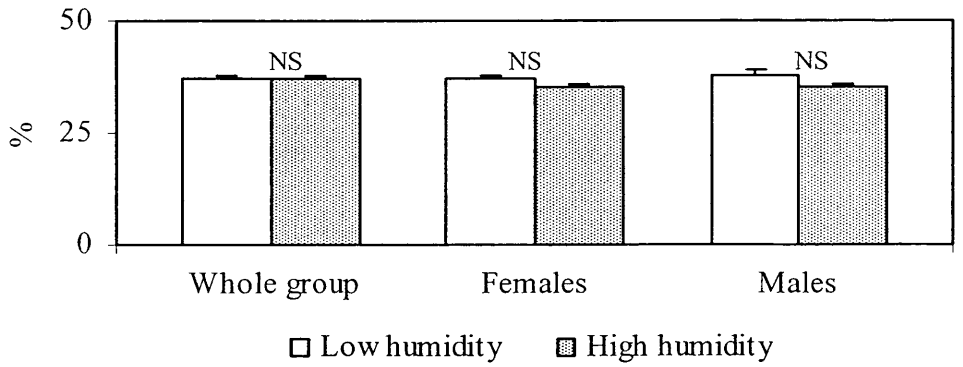


Figure 3.2: Percentage of time spent grooming by the study animals under condition of lower (26-61%) and higher (62-96%) relative humidity (means ± SE).



b) Self-grooming.

Time of day had a significant influence on self-grooming in the whole group ($F = 2.873$, $df = 8/2106$, $p < 0.005$) and in males ($F = 1.963$, $df = 8/910$, $p < 0.05$). Most self-grooming occurred in the early morning, with a second minor peak between 15.00 and 16.00 hrs. Conversely, females displayed self-grooming similarly in the different hours of the day ($F = 1.270$, $df = 8/1203$, NS).

Temperature did not affect self-grooming when data collected in the different hours of day were lumped for the whole group (main effect of Temperature: $F = 0.018$, $df = 1/2073$, NS, Temperature x Individual identity interaction: $F = 1.432$, $df = 20/2073$, NS), in females (Table 3.5) or in males either (Table 3.6). Considering that ambient temperature presents obvious diurnal variations, and that self-grooming of all Nina A members and of the males was influenced by time of day (see above), I decided to add time of day as a categorical variable in the ANCOVA for the whole group and for the males. The main effect of temperature remained non significant, but significant two- and three-way interactions emerged for both the categories (Table 3.4 for the whole group and Table 3.6 for males). These interactions are not easy to interpret, as they seem to indicate that the effects of temperature on self-grooming differed in the different individuals and in the different hours of day. Overall, however, self-grooming did not seem to be completely independent from the influences of ambient temperature. Indeed, a Wilcoxon test comparing self-grooming recorded under conditions of lower and higher temperatures revealed significantly more self-grooming under higher temperatures in Nina A group as a whole ($T = 6$, $N = 15$, $p < 0.005$) and in males ($T = 28$, $N = 7$, $p < 0.05$). A Wilcoxon test indicated a similar trend among female macaques but the comparison did not quite reach significance ($T = 30.5$, $N = 8$, $p < 0.07$; Figure 3.3).

Relative humidity did not affect self-grooming of the whole group when data collected in the different hours of day were lumped (main effect of Humidity: $F = 2.096$, $df = 1/2073$, NS, Humidity x Individual identity interaction: $F = 0.690$, $df = 20/2073$, NS). Again, when time of day was added to the ANCOVA, significant two- and three-way interactions emerged (Table 3.4). Relative humidity tended to affect self-grooming in females (Table 3.5). Moreover, for females no significant interaction was found between humidity and individual identity (Table 3.5). Relative humidity did not influence male self-grooming (Table 3.6). However, when time of day was added to the ANCOVA for male macaques, significant two- and three-way interactions emerged (Table 3.6). Self-grooming was thus influenced in complex ways also by relative humidity. Comparing self-grooming recorded under conditions of higher and lower relative humidity revealed a

significant difference in the whole group (T = 9, N = 14, $p < 0.01$) as well as in females (T = 36, N = 8, $p < 0.05$). The test was not significant in male macaques (T = 16.5, N = 6, NS) (Figure 3.4).

Table 3.4: The effect of ambient temperature and relative humidity on self-grooming for all Nina A group members (N = 21; * $p < 0.002$; ** $p < 0.0001$).

Climatic factor	Effect	F value, d.f and significance
Temperature		
	Temperature	0.00 (1/1527), NS
	Individual identity	2.52 (14/1527) *
	Time of day	0.85 (8/1527), NS
	Temperature x Individual identity	2.45 (14/1527) *
	Time of day x Temperature	0.86 (1/1527), NS
	Individual identity x Time of day	2.10 (112/1527) **
	Individual identity x Time of Day x Temperature	2.42 (112/1527) **
Humidity		
	Humidity	2.49 (1/1527), NS
	Individual identity	1.05(14/1527), NS
	Time of day	5.85 (8/1527) **

	Humidity x Individual identity	1.04 (14/1527), NS
	Time of Day x Humidity	5.76 (8/1527) **
	Individual identity x Time of Day	1.80 (112/1527) **
	Individual identity x Time of Day x Humidity	1.99 (112/1527) **

Table 3.5: The effect of ambient temperature and relative humidity on self-grooming for Nina A females (N = 8).

Climatic factor	Effect	F value, d.f and significance
Temperature		
	Temperature	2.67 (1/1203), NS
	Individual identity	0.51 (7/1203), NS
	Temperature x Individual identity	0.30 (7/1203), NS
Humidity		
	Humidity	3.32 (1/1203), NS
	Individual identity	0.09 (7/1203), NS
	Humidity x Individual identity	0.21 (7/1203), NS

Table 3.6: The effect of ambient temperature and relative humidity on self-grooming for Nina A males (N = 13; * $p < 0.05$; ** $p < 0.005$; *** $p < 0.001$).

Climatic factor	Effect	F value, d.f and significance
Temperature		
	Temperature	0.22 (1/910), NS
	Individual identity	1.96 (12/910) *
	Time of day	1.49 (8/910), NS
	Temperature x Individual identity	1.97 (12/910) *
	Time of day x Temperature	1.49 (8/910), NS
	Individual identity x Time of day	1.95 (88/910) **
	Individual identity x Time of Day x Temperature	2.20 (89/910) ***
Humidity		
	Humidity	1.09 (1/910), NS
	Individual identity	1.24 (12/910), NS
	Time of day	2.56 (8/910) **
	Humidity x Individual identity	1.19 (12/910), NS
	Time of Day x Humidity	2.58 (8/910) **

Individual identity x Time of Day	1.68 (90/910) **
Individual identity x Time of Day x Humidity	1.85 (90/910) **

Figure 3.3: Percentage of time spent self-grooming by the study animals under condition of lower (8-21°C) and higher (22-34°C) ambient temperature (means ± SE).

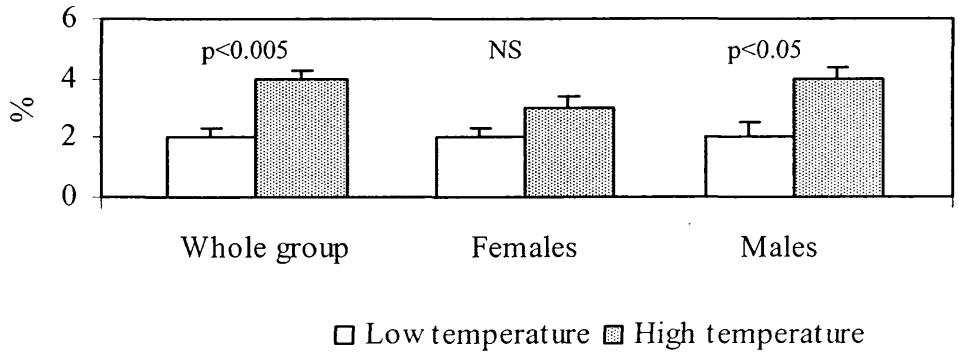
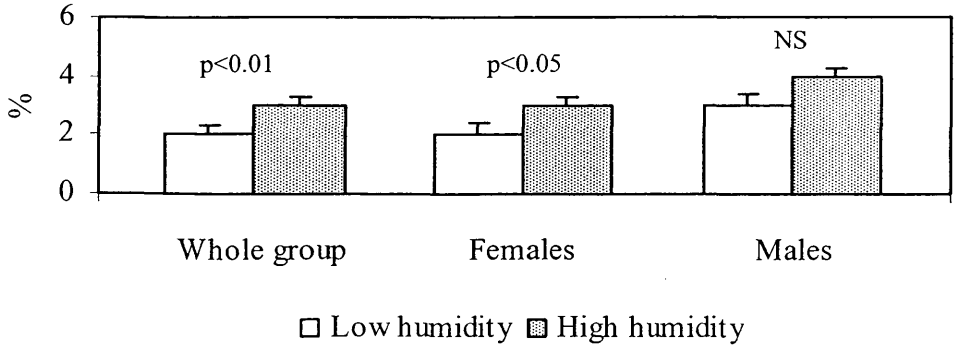


Figure 3.4: Percentage of time spent self-grooming by the study animals under condition of lower (26-61%) and higher (62-96%) relative humidity (means ± SE).



c) Scratching.

Time of day had no significant influence on the rate of scratching (whole group: $F = 0.377$, $df = 8/2106$, NS; females: $F = 1.525$, $df = 8/1203$, NS; males: $F = 0.513$, $df = 8/910$, NS).

Increasing ambient temperatures were associated with increasing rates of scratching for the whole group (Table 3.7) and for both the sex classes (Table 3.8 for females and Table 3.9 for males, respectively). This effect did not vary among the different individuals analysing the whole group (Table 3.7) and the males (Table 3.9). On the contrary, individual identity had a significant effect for females (Table 3.8). Confirming the above result, significantly more scratching was recorded under conditions of higher than lower temperatures (whole group: $T = 0$, $N = 15$, $p < 0.001$; females: $T = 36$, $N = 8$, $p < 0.05$; males: $T = 28$, $N = 7$, $p < 0.05$; Figure 3.5).

Similarly, increasing relative humidity was associated with increasing rates of scratching (Table 3.7 for the whole group; Table 3.8 for females and Table 3.9 for males, respectively). Once again this effect did not vary among the different individuals of the whole group (Table 3.7) or among the males (Table 3.9). Differently, it varied among the different female individuals (Table 3.8). Finally, more scratching was recorded under conditions of higher than lower humidity (whole group: $T = 0$, $N = 14$, $p < 0.005$; females: $T = 36$, $N = 8$, $p < 0.012$; males: $T = 21$, $N = 6$, $p < 0.027$; Figure 3.6).

Since in our sample ambient temperature and relative humidity were positively correlated (whole group: $r = 0.56$, $N = 2113$, $p < 0.001$; females: $r = 0.56$, $N = 1203$, $p < 0.0001$; males: $r = 0.554$, $N = 910$, $p < 0.0001$) I tried to disentangle their independent contributions to the observed variations in scratching rates. I therefore ran three multiple regressions including both temperature and relative humidity as independent variables. The overall regression was highly significant for the whole group ($r = 0.297$, $p < 0.0001$) and both temperature and relative humidity had significant independent effects ($t = 8.057$, $p < 0.0001$, and $t = 5.301$, $p < 0.0001$, respectively). The same results were obtained when a multiple regression was run for the two sex classes (females: $r = 0.321$, $F = 68.796$, $p < 0.0001$; Temperature: $t = 7.425$, $p < 0.0001$; Humidity: $t =$

3.359, $p < 0.001$; males: $r = 0.252$, $F = 30.776$, $p < 0.0001$; Temperature: $t = 3.426$, $p < 0.001$; Humidity: $t = 3.975$, $p < 0.0001$). Note, however, that such analysis cannot control for the influence of inter-individual variations.

Table 3.7: The effect of ambient temperature and relative humidity on scratching for all Nina A group members (N = 21; * $p < 0.0001$).

Climatic factor	Effect	F value, d.f and significance
Temperature		
	Temperature	60.84 (1/2073) *
	Individual identity	1.12 (20/2073), NS
	Temperature x Individual identity	1.24 (20/2073)
Humidity		
	Humidity	38.35 (1/2073) *
	Individual identity	0.92 (20/2073), NS
	Humidity x Individual identity	1.26 (20/2073)

Table 3.8: The effect of ambient temperature and relative humidity on scratching for Nina A females (N = 8; * $p < 0.05$; ** $p < 0.0001$).

Climatic factor	Effect	F value, d.f and significance
Temperature		
	Temperature	135.8 (1/1203) **
	Individual identity	0.89 (7/1203), NS
	Temperature x Individual identity	2.25 (7/1203) *
Humidity		
	Humidity	79.88 (1/1203) **
	Individual identity	1.31 (7/1203), NS
	Humidity x Individual identity	2.52 (7/1203) *

Table 3.9: The effect of ambient temperature and relative humidity on scratching for Nina A males (N = 13; * $p < 0.0001$).

Climatic factor	Effect	F value, d.f and significance
Temperature		
	Temperature	23.5 (1/910) *
	Individual identity	1.08 (12/910), NS
	Temperature x Individual identity	0.82 (12/1203), NS
Humidity		
	Humidity	12.65 (1/910) *
	Individual identity	0.75 (12/910), NS
	Humidity x Individual identity	0.67 (12/910), NS

Figure 3.5: Frequency of scratching of the study animals under condition of lower (8-21°C) and higher (22-34°C) ambient temperature (means ± SE).

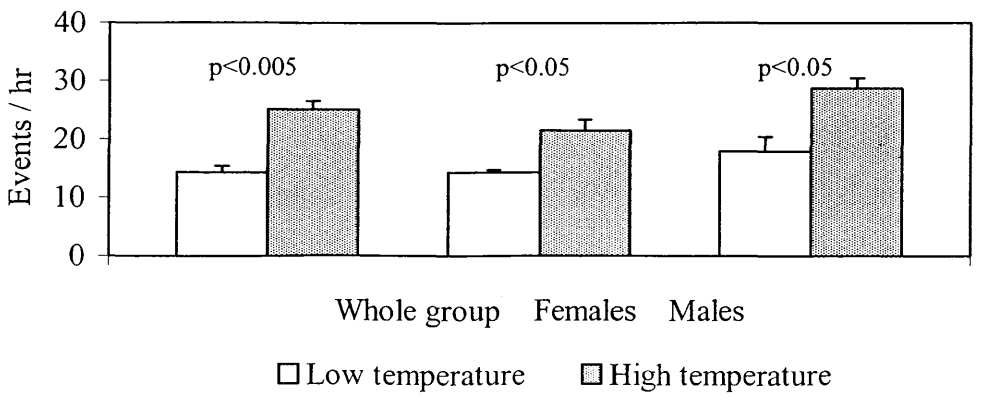
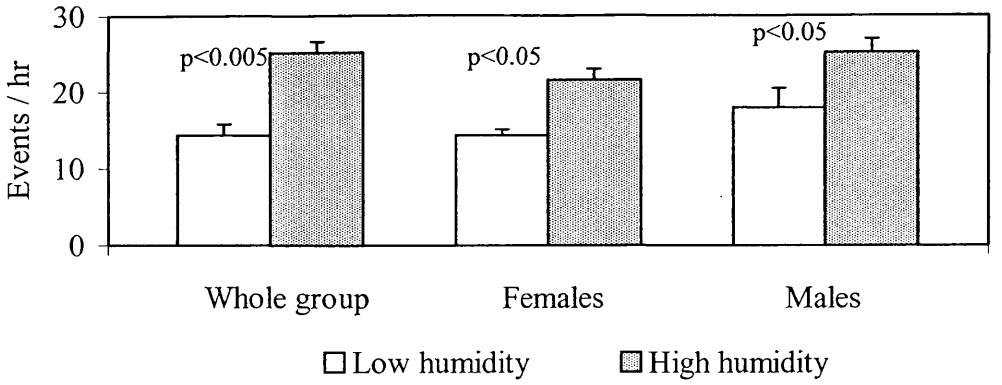


Figure 3.6: Frequency of scratching of the study animals under condition of lower (26-61%) and higher (62-96%) relative humidity (means ± SE).



3.4 Discussion.

The results of this study show that, in wild Japanese macaques, weather variations exerted differential effects on the various behaviours involved in the maintenance of the pelage. Scratching in both female and male macaques was considerably affected by variations in ambient temperature and humidity. Self-grooming also appeared to be influenced by these climatic factors, although less consistently. Indeed, temperature and humidity had a different impact on self-grooming behaviour of the two sex classes. The significant two- and three-way interactions observed between self-grooming, temperature/humidity, time of day and individual identity of male macaques are difficult to interpret, but may be due to the different amount of grooming exchanged by different monkeys. Animals who receive less grooming might require a greater amount of self-grooming for the maintenance of the pelage. It is, however, difficult to provide a convincing account for the observed statistical interactions.

Analysis of covariance showed that ambient temperature influenced grooming behaviour in female macaques. However, this result was controversial. Indeed, when data were split in order to investigate the differences in grooming

exchanged during the mating and non-mating seasons, the significant effect of ambient temperature on the time spent grooming by the females emerged only during the mating season. In Yakushima the mating season lasts more or less four months a year and occurs in late summer / early winter (from end of August to end of December). Moreover, Wilcoxon tests comparing grooming under conditions of lower and higher temperatures indicated the absence of a significant effect of ambient temperature on female grooming. Male macaques performed similar amount of grooming despite varying ambient temperatures and this result emerged analysing data from all the members of the study group too. Relative humidity did not affect grooming activity in either males or females. Hence, overall, social grooming seemed to be relatively independent of these environmental factors.

Seasonal variations in grooming, self-grooming and scratching might be explained by trade-offs between pelage care and other activities such as feeding and travelling. For example, time devoted to pelage care could increase when animals spend less time feeding (e.g. in periods of high food availability). The results of this study, however, contrast with this explanation. In fact, if time budget trade-offs were at the basis of the present results, then stronger effects should have been observed on grooming (the most time-consuming of the behaviours observed), while no effect would be expected on scratching (an essentially instantaneous behaviour with no time budget constraints). The pattern of results observed is the opposite of what is predicted by time budget trade-offs, and it could be therefore concluded that direct influences on pelage care needs constitute a more likely explanation. Previous studies, on captive long-tailed macaques, led to the same conclusion (Troisi and Schino, 1986).

Self-grooming and scratching are considered to be reliable behavioural indicators of stress, as their frequency increases or decreases in monkeys injected with, respectively, stress-inducing or stress-decreasing drugs (e.g. Schino *et al.*, 1996). This factor should again favour self-grooming and scratching being independent from environmental conditions. More likely, stressful events (e.g. conflicts) are often unpredictable and often of short duration, so that their effect

on self-grooming and scratching may be not as important as ambient temperature or humidity.

Earlier research had demonstrated that in long-tailed macaques, a species confined to South-East tropical Asia, grooming is as sensitive to weather variations as the other behaviours related to the maintenance of the pelage: they all increase under conditions of high temperature and/or humidity (Troisi and Schino, 1986, 1987; Pavani *et al.*, 1991). Troisi and Schino (1986) speculated that, given the social function of grooming, adaptation of macaques to temperate climates may have required the emancipation of grooming from the proximate influence of variations in ambient temperature and humidity. This study partly supported this hypothesis. Moreover, it suggested that self-grooming and scratching (that share with grooming its hygienic, but not its social function) may have in contrast retained their original sensitivity to environmental influences.

In other words, data indicate that differences in the ultimate functions of grooming and self-grooming/scratching may translate into differences in their proximate causation, namely into a differential sensitivity to environmental influences. Thus, while variations in the need for pelage care are presumably associated with changes in ambient temperature and humidity, these seem to affect mostly self-grooming and scratching. Grooming, although still having an important hygienic function (Tanaka and Takefushi, 1993; Zamma, 2002), is primarily a social behaviour whose complete dependence on ambient temperature and humidity would interfere with its role in mediating inter-individual relationships. Adaptation of Japanese macaques to the temperate/subtropical climate of their present range may thus have required a readjustment of the proximate causation of some of its behaviours. Self-grooming and scratching, with a primarily hygienic function, retained their sensitivity to the stimuli provided by the pelage (e.g. sweating or presence of ectoparasites) and thus remained influenced by abiotic environmental conditions. Conversely, grooming, which has both hygienic and social functions, became more independent from the influence of climatic variations, in order not to jeopardise its social function. For example, a reduction in grooming during the cold winter months would conflict with its critical role in regulating inter-individual relationships during the mating

season. Interestingly among wild impalas (*Aepyceros melampus*), where grooming plays no social function, grooming, self-grooming and scratching show similar seasonal variations correlated with the intensity of tick challenge (Mooring, 1995). However, in chacma baboons (*P. cynocephalus*), living in a coastal reserve in South Africa, grooming activity was affected by temperature and humidity, despite the considerable seasonal variation in both rainfall and temperature experienced by this species, due to the southerly latitude of its habitat (Hill *et al.*. 2004). Therefore, more specific studies on different species of macaques are needed to corroborate the hypothesis proposed to interpret the present data on grooming. In particular, it would be useful to carry out a field work on *M. sylvanus*, living in Morocco, Algeria and Gibraltar, with a temperate climate similar to Japan to investigate if selection pressures that favour liberation of grooming from the influence of climatic factors have operated in this species too.

In macaques, whether the influence of ambient temperature and humidity on pelage care is mediated through variations in piloerection, sweating, abundance of ectoparasites, or other mechanisms is presently unknown and warrants further investigation. Seasonal variations in the presence of ticks in the environment and in the degree of infestation of monkeys were reported by Rajagopalan and Anderson (1971, in *M. radiata* and *Presbytis entellus*) and Saunders and Hausfater (1988, in *P. cynocephalus*). The latter also reported that frequency of grooming in baboons was not correlated with tick challenge, but did not report data on self-grooming or scratching. Japanese macaques are mainly infected by lice, *Pedicinus obtusus* and *P. eurygaster* (Kaneko, 1971, cited in Tanaka and Takefushi, 1993). Zamma (2002) estimated that an adult Japanese macaque harbours an average of 500 louse eggs and reported that both self-grooming and grooming were primarily directed at those sites of the body that were more heavily infested. Given that lice, in contrast to ticks, complete their life cycle on the body of their host, it is possible that seasonal variations in their degree of infestation are comparatively smaller. Moreover, the observations conducted in captive parasite-free environments suggest that variations in ambient temperature/humidity may affect pelage care also independently of the presence of parasites (Troisi and Schino, 1986; 1987; Pavani *et al.*, 1991). To summarise,

the scant available data do not seem to support the notion that variations in pelage care associated with ambient temperature/humidity are mediated by variations in ectoparasite challenge. The role of piloerection and sweating remains to be investigated.

Studies of evolutionary ecology have traditionally neglected issues related to the proximate causation of behaviour to concentrate on ultimate function. Adaptation, however, often involves a restructuring of the causal relations underlying behaviour so as to modify responsiveness to environmental/ecological stimuli (e.g., Gould, 1982). Adding information on the proximate determinants of behaviour will thus contribute to enhancing our understanding of the ecology and adaptation of primates to their environment.

CHAPTER 4

GROOMING RECIPROCATION AND INTERCHANGE: TWO DIFFERENT ANALYTICAL APPROACHES

Chapter 3 showed that grooming is relatively independent from climatic changes. In the rest of the Thesis I only focus on grooming distribution among macaque females as a measure of the quality of, and investment in the social relationships, as male-female or male-male long-lasting amicable relationships are rarely observed in Japanese macaques. For example, male-female grooming is often observed during consortships (see Chapter 1) but is infrequently observed outside this context. Moreover, males are the dispersing sex in this species (see Chapter 1) and thus have little opportunity or need for long-term amicable relationships with one another. In this chapter I use two analytical methods (one based on dyads and the other on matrices) to study grooming reciprocation (see Table 1.1 for a definition). I aim to determine if and how the two methods support various predictions on grooming distribution of the biological market theory. Moreover, I aim to discuss the effectiveness of the two methods employed for studies on grooming distribution. If one method can be shown to be more appropriate for studies on grooming distribution, this will be used (in Chapters 5 to 7) to analyse the effect of seasonal changes and group size on grooming distribution and the benefits of grooming. Subjects of this study were the eight females living in Nina A group.

4.1 Introduction.

In Chapter 1 I reviewed the available literature showing that grooming can inflict costs on the fitness of individuals performing it, in terms of reduced attention to predators' attacks or time available for resting (Cords, 1995; Dunbar, 1992; Dunbar and Sharman, 1984; Mooring and Hart, 1995). At the same time,

however, many studies have shown the possible beneficial effects of grooming exchange (this will also be the topic of Chapter 7): ectoparasite removal, reduced stress, increased tolerance near valuable resources, and agonistic support (Feh and de Mazieres, 1993; Henzi and Barrett, 2002; Kapsalis and Berman, 1996; Mooring *et al.*, 1996; Saunders and Hausfater, 1988). This is examined in detail in other chapters (mainly Chapter 1, 7 and 8), and see them for an extensive discussion on the importance of grooming for social relationships.

Barrett and colleagues (Barret *et al.*, 1999; 2000) investigated the degree of grooming reciprocation in chacma baboons (*Papio cynocephalus ursinus*) and the applicability of the biological market theory in this species. They analysed the time contribution of the partners within each observed grooming bout, hence at dyadic level. In other words, they only considered immediately reciprocated or non-reciprocated grooming in their analyses. Then, the authors randomly selected a grooming interaction for each dyad (reciprocated or not, depending on the analysis performed) and ran a series of Spearman rank correlations. For example, to determine whether grooming was reciprocated or not, Barrett and colleagues (1999) correlated the amount of grooming given by each female to her grooming partners with the amount of grooming she received in exchange as soon as she stopped grooming that female. Statistical dependency is one of the problems that arise when reciprocity is analysed within pairs, as study subjects may reoccur in several dyads (Everitt, 1996). Choosing exclusive pairs, as done by Barrett and colleagues (1999), may be a method to reduce this problem. However, the sample size is still inflated even when this procedure is followed and so this method gives not completely reliable results.

Social interactions may also be studied successfully at group level (i.e. among dyads) as described by Hemelrijk (1990). Data are summed over a certain time period and represented in matrices in which rows and columns stand for individuals. Matrix comparison by means of the row-wise Kr-test takes the individual differences in tendencies into account, as correlations are only performed within every row (individual) and combined over all rows. Moreover, matrix correlations do not inflate sample size.

Barrett and colleagues (1999) presupposed that when individuals exchange grooming for other grooming, the groomee returns the quantity of received service as soon as the groomer stops performing it, in order to circumvent cheating. On the other hand, females that do not reciprocate grooming at once would exchange it for other commodities. Therefore, these authors state that different temporal patterns of grooming discriminate reciprocal and interchange traders (Schino *et al.*, 2003). However, I recently showed (Schino *et al.*, 2003) that, at least in captive female Japanese macaques, the temporal pattern used to distinguish different classes of traders may not be reliable: immediately reciprocated and non-reciprocated grooming did not significantly differ in their patterns of distribution. Moreover, total amount of grooming exchanged within dyads was highly reciprocated; a finding that does not support the assumption that immediate reciprocation is a necessary strategy to avoid cheating.

It is a matter of debate whether grooming interactions have to be analysed at the dyadic level or using matrices (e.g. Manson *et al.*, 1999). Moreover, there is a general disagreement on the timing of grooming exchange: some authors postulate that each grooming interaction between two animals is independent from the others while others consider social interactions within a longer time window as the unit of analysis (de Vries, 1993).

With this background in mind, this Chapter aimed to analyse grooming distribution and reciprocation using two different analytical approaches: one based on dyads and using single grooming interactions, as proposed by Barrett and colleagues (e.g. Barret *et al.*, 1999), and the other based on row-wise matrix correlation and using overall grooming exchanged between two monkeys (Hemelrijk, 1990; de Vries, 1993). It aimed to discuss and compare the efficacy of these two methods for studies on grooming distribution by testing various predictions of the biological market theory. According to this theory, high-ranking animals are able to monopolise resources for which low-ranking individuals can trade grooming (see Chapter 1 for details of the biological market theory). For this reason, more non-reciprocal grooming should go up the hierarchy rather than down. At the same time, closely ranking individuals should show more balanced grooming distribution compared to distantly ranking ones. Indeed, between

closely-ranking individuals the power differential is small, making them unable to interchange anything. Consequently, they should engage in more reciprocal (balanced) grooming and less interchange (one-sided) grooming. In particular the following six predictions of the biological market theory will be tested:

1) Grooming will be directed more up than down the hierarchy.
2) Grooming given and received will be positively correlated.
3) Reciprocal and non-reciprocal grooming exchanged within a dyad will not be correlated
4) High-ranking females will receive as much reciprocal grooming as low-ranking females, while more non-reciprocal grooming will be directed up rather than down the hierarchy.
5) The degree of grooming reciprocation will be negatively correlated with the rank distance between the partners.
6) Females will devote an equal amount of reciprocal grooming to distantly and to closely ranking partners but they will give more non-reciprocal grooming to distantly ranking partners.

Each prediction will be first tested at dyadic level (i.e. Method A) using single grooming interactions and a series of Spearman rank correlations (see below). Then it will also be tested at group level (i.e. Method B) using total grooming exchanged between females and a series of row-wise Kr-tests. Moreover, for each prediction and for each analytical approach the analysis will first be run using the whole sample size and then re-run excluding kin females, to control for the effect of kinship on grooming distribution.

4.2 Methods.

a) Study subjects and data collection.

Each of the eight adult females belonging to Nina A group (see Chapter 2) were the subjects of 160 focal animal 10-minute observation sessions (Altmann, 1974; Martin and Bateson, 1993). The duration of all the grooming bouts as well as the groomers' and groomees' identity were recorded. Percentages of time spent grooming by the females were calculated using these data. Females were ordered

in a linear hierarchy analysing the outcomes of decided agonistic interactions and the direction of submissive signals. The following analyses are based on 207.3 hrs of focal observations on the eight subjects of this study (see Chapter 2).

I designated as "reciprocal", *sensu* Barrett *et al.* (1999), two consecutive grooming episodes in which female 1 grooms female 2 and as soon as female 1 stops female 2 commences grooming (see Section 2.2b). On the other hand, I defined a "non-reciprocal grooming bout" as a grooming session after which the groomer did not receive grooming from her partner immediately. Even though within a single focal animal session more than one alternation of roles between the partners could occur, I selected only the first reversal for analysis of time contributions. The reason for this was that only a small proportion of the 10-min focal observations (i.e. 29.3%) gathered did include the full sequence of grooming episodes in which the actors became the recipients of grooming. Therefore, most of the grooming interactions had to be discarded (see Chapter 2 for the reason why 10-minute focal observations were collected). Consequently, even more observations would have been discarded if time matching had to be calculated across the sequence as a whole (as Barrett *et al*, 2002 did) and this procedure would have considerably biased the sample. By selecting the first grooming reversal only, possible bias in the sample was reduced. Within the grooming performed that was recorded from the beginning to the end, immediately reciprocated grooming comprised 61% of total grooming given by the females, while 39% of observed grooming was non-reciprocated.

b) Data analysis.

I tested each of the above predictions using two different statistical approaches. First, I analysed grooming distribution using scores per dyad with a series of Spearman rank correlations. Following Barrett and colleagues (1999), I identified all the grooming interactions that each single female macaque had with her female companions. I then selected at random one grooming interaction between two females among all those available for that particular dyad. Following this method I tested for the relationship between reciprocated and non-

reciprocated grooming and for their distribution in relation to the ranks of the grooming partners. To control for any effect of kinship on grooming distribution, all the Spearman correlations were re-run, this time excluding kin dyads from the analyses.

Matrix comparisons by means of the row-wise Kr-test were used as an alternative analytical method to test the same six predictions. Kendall's row-wise matrix correlation coefficients (Tau_{rw}) and the corresponding probability values based on 10,000 random permutations were calculated using MatMan for Windows, a program for the analysis of sociometric matrices (de Vries, 1993). The value in each cell corresponded to the total time (including the episodes of which I did not see the start and/or the end) in which the row female was observed grooming the column female during focal samples of either of the two individuals, corrected by the seconds of focal sampling for each female of the dyad (i.e. time that A groomed B / observation time A + observation time B). In a similar way I created matrices with percentages of time spent in immediately reciprocated and non-reciprocated grooming by each female to others all year round. As for the previous analytical method, I re-ran all the matrix correlatios to control for the effect of kinship. To this end, I used a series of partial matrix correlations where the control matrix contained the kin relationships between the females (i.e. in each cell was entered 1 if the two females were kin and 0 if they were not related).

To briefly summarise, the two analytical approaches significantly differed one from the other: Spearman correlations were run using randomly selected grooming episodes for each dyad whereas matrix correlations were run using the total amount of grooming observed for each dyad.

When I analysed the effect of rank of the groomee, I assigned rank 1 to the highest ranking female, rank 2 to the next highest ranking female and so on until rank 8, which was given to the lowest ranking female. For the analyses on rank distance between the grooming partners, I subtracted the rank of the groomee from the rank of the groomer. Following this procedure, rank distance could either be a positive or a negative figure depending on the role each female had during the grooming interaction. For example, rank distance between two females ranking first and fourth, respectively, was -3 if the first ranking female was the

groomer and 3 if she was the groomee. Given that this approach is not completely reliable (see Prediction 5 below for an explanation) I also, exclusively for Prediction 6, used the unsigned rank distance between the grooming partners, regardless of which female was the groomer or the groomee.

4.3 Results.

Prediction 1: Grooming will be directed more up than down the hierarchy.

Method A (dyads).

First, I analysed the relationship between the grooming given by each female and the rank of the groomee at the dyadic level, thus following Barrett *et al.*'s method (1999). Grooming and rank of the groomee were not significantly correlated (Spearman correlation: $r_S = -0.075$, N = 44, NS; Figure 4.1). A similar, non-significant result was obtained when dyads of kin females were excluded from the analysis ($r_S = -0.206$, N = 40, NS).

Method B (matrix).

Grooming given was then measured using row-wise matrix correlations following the method proposed by Hemelrijk (1990). To this end, I correlated a matrix containing the total amount of grooming given by each monkey to the other female partners and a matrix containing the rank of the groomee (Table 4.1 a, b). Female macaques significantly directed grooming up the hierarchy ($Tau_{rw} = -0.261$, $p < 0.05$), and this trend became even stronger when kinship was partialled out ($Tau_{rw,xy,z} = -0.366$, $p < 0.005$).

Interpretation.

The prediction was supported when grooming was analysed using matrices but not when using Spearman correlations on dyadic scores. The results obtained with matrices thus suggest the possibility of interchange trading of grooming, as predicted by the biological market theory, in Japanese macaques (i.e. a species characterised by strict dominance relationships).

Figure 4.1 Relation between the duration of grooming given (seconds) and rank of the groomee.

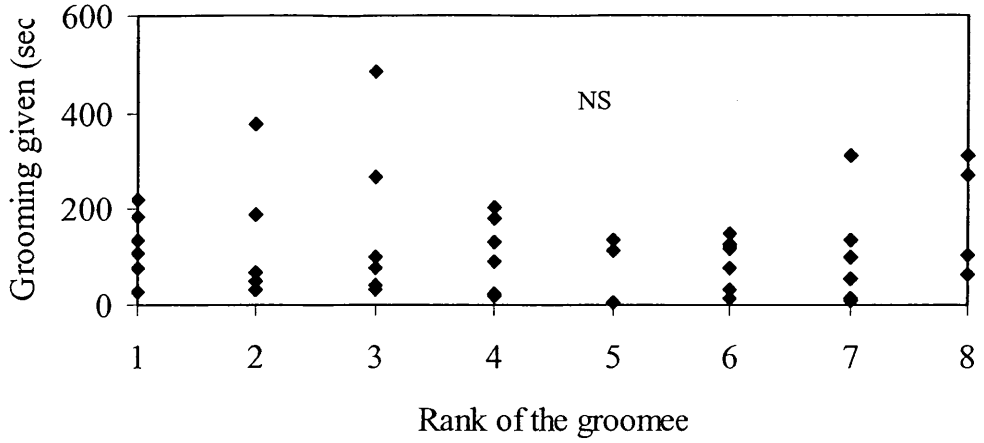


Table 4.1: Matrices containing, respectively, the amount of grooming given (% of observation time) among females (a) and the rank of the female groomee (b) (*close-kin females in Nina A group).

(a)

Monkey	Sya	Shi	Han	Ram	Hot	Htu	Yam	Yri
Sya		1.65	3.26	0.50	0.34	0	1.03	0.49
Shi	6.85		9.19	2.90	0.60	0	0.94	0.19
Han	1.79	5.81		0.95	0.14	0.11	0.41	0.09
Ram	1.87	6.14	6.81		6.79	2.95	4.03	0.66
Hot	3.21	1.20	2.21	7.28		10.34*	1.79	0.35
Htu	0.41	0.18	0.63	3.47	7.54*		0.12	1.22
Yam	3.55	2.54	5.31	1.52	0.85	0.05		56.25*
Yri	1.27	0.75	0.84	0.07	0	0.41	11.22*	

(b)

Monkey	Sya	Shi	Han	Ram	Hot	Htu	Yam	Yri
Sya		2	3	6	7	8	4	5
Shi	1		3	6	7	8	4	5
Han	1	2		6	7	8	4	5
Ram	1	2	3		7	8	4	5
Hot	1	2	3	6		8*	4	5
Htu	1	2	3	6	7*		4	5
Yam	1	2	3	6	7	8		5*
Yri	1	2	3	6	7	8	4*	

Prediction 2: Grooming given and received will be positively correlated.

Method A (dyads).

Following Barrett *et al.*'s method (1999) I correlated the amount of grooming given and received in each immediately reciprocated grooming session. Female macaques did not exchange a comparable amount of immediately reciprocated grooming (r_S = 0.027, N = 44, NS; Figure 4.2). Excluding dyads of kin females from the analysis confirmed the lack of time matching (r_S = - 0.060, N = 40, NS).

Method B (matrix).

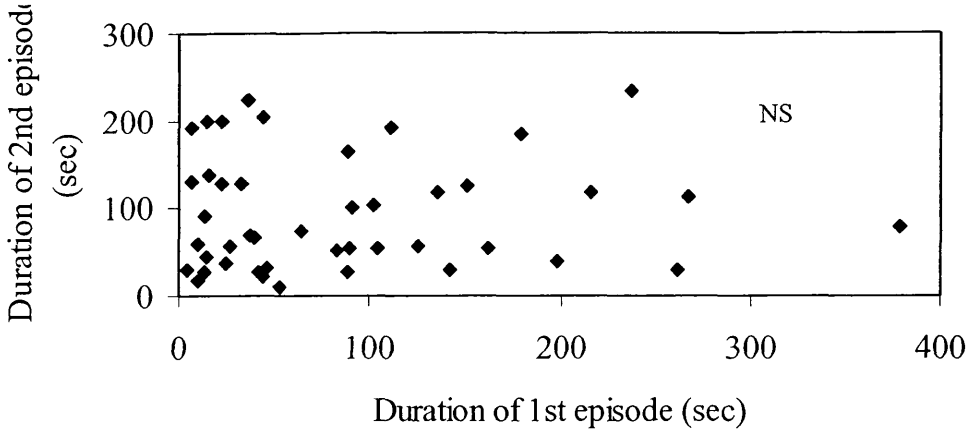
On the other hand, a row-wise matrix correlation between the matrix of total grooming given (Table 4.1a) and its transposition (grooming received) revealed that females did reciprocate the overall amount of grooming they were given (Tau_{rw} = 0.507, $p < 0.0001$). Partialling out the effect of kinship did not substantially alter the significance of the correlation ($Tau_{rw,xy,z}$ = 0.425, $p < 0.001$).

Interpretation.

As for prediction 1, the analyses run using matrices supported prediction 2 while those done using dyads did not. Therefore, total grooming appeared to be reciprocated, whereas I found no evidence of immediate reciprocation within

each grooming episode. This result did not support the findings of Barrett and colleagues (1999).

Figure 4.2: Relation between the first and second grooming episode (seconds).



Prediction 3: Reciprocal and non-reciprocal grooming will have different allocation.

Method A (dyads).

Reciprocal and non reciprocal grooming were not significantly related when analysed at the dyadic level ($r_S = 0.284$, N = 44, NS; Figure 4.3). The correlation remained non-significant when dyads of kin females were excluded ($r_S = 0.2444$, N = 31, NS).

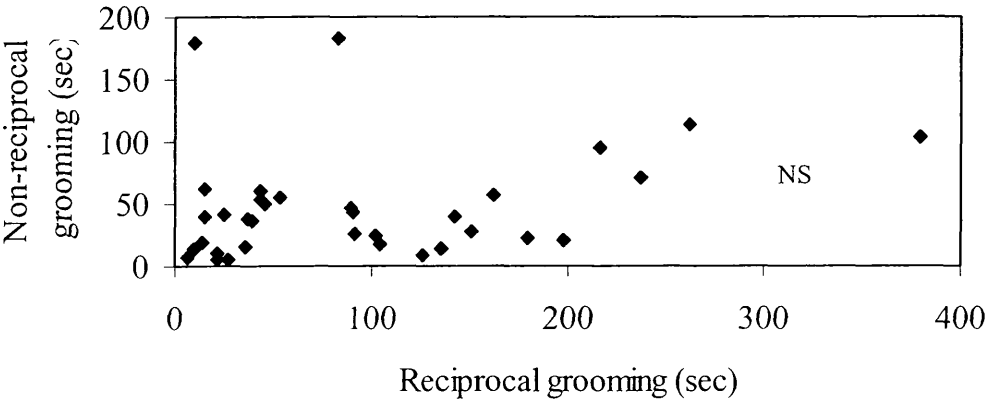
Method B (matrix).

The matrices of overall reciprocal and non-reciprocal grooming were significantly correlated ($Tau_{rw} = 0.549$, $p < 0.001$; Appendix B.1 and B.2 at the end of this thesis). Similarly, a significant positive correlation was found when excluding kin from the analysis ($Tau_{rw,xy,z} = 0.473$, $p < 0.001$).

Interpretation.

The interpretation is a bit more complex here as the method used by Barrett and colleagues supported prediction 3 whereas it was not supported by the results of the matrix correlation. Indeed, this approach showed a positive significant correlation between the two types of grooming.

Figure 4.3: Relation between the duration of reciprocal and non-reciprocal grooming (seconds).



Prediction 4: High-ranking females will receive as much reciprocal grooming as low-ranking females, while more non-reciprocal grooming will be directed up than down the hierarchy.

Method A (dyads).

Supporting this prediction, reciprocal grooming was not significantly related to the rank of the groomee (r_S = 0.028, N = 44, NS; Figure 4.4). On the contrary the prediction regarded non-reciprocal grooming was not supported (r_S = -0.063, N = 35, NS; Figure 4.5). When dyads of kin females were excluded from the analyses the results remained non-significant for both reciprocal grooming (r_S = -0.097, N = 40, NS) and non-reciprocal grooming (r_S = -0.171, N = 31, NS).

Method B (matrix).

When using matrix correlation, it initially appeared that there was no relation between rank and reciprocal grooming (Tau_{rw} = - 0.107, NS; Table 4.1b and Appendix B.1). However, when partialling out the effect of kinship, it emerged that females gave more reciprocal grooming to higher-ranking, non-related group mates ($Tau_{rw,xy,z}$ = - 0.197, $p < 0.05$). Finally, female macaques directed more non-reciprocal grooming up rather than down the hierarchy (Tau_{rw} = - 0.270, $p < 0.05$). Partialling out the effect of kinship increased the significance of this correlation ($Tau_{rw,xy,z}$ = - 0.377, $p < 0.001$).

Interpretation.

The correlations run using scores per dyad only partially supported prediction 4. Matrix correlations partially supported this prediction too: non-reciprocal grooming was directed up the hierarchy (supporting prediction 4) but the same happened for reciprocal grooming (contrasting with prediction 4).

Figure 4.4: Relation between the duration of reciprocal grooming (seconds) and the rank of the groomee.

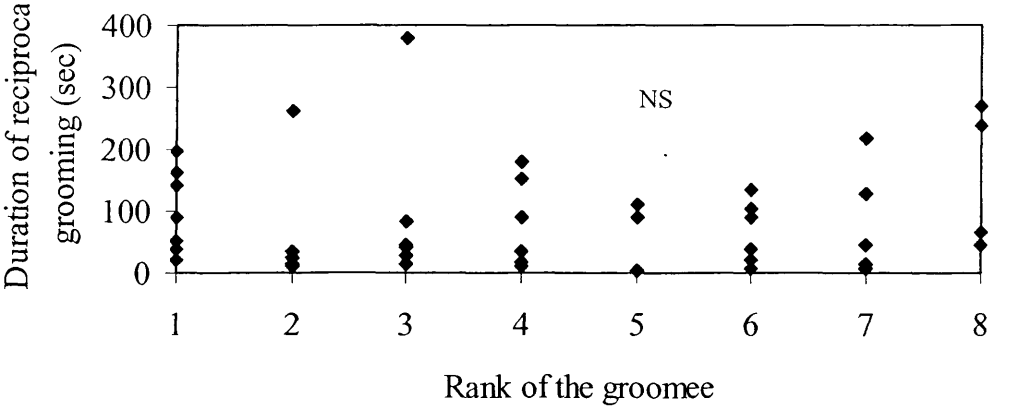
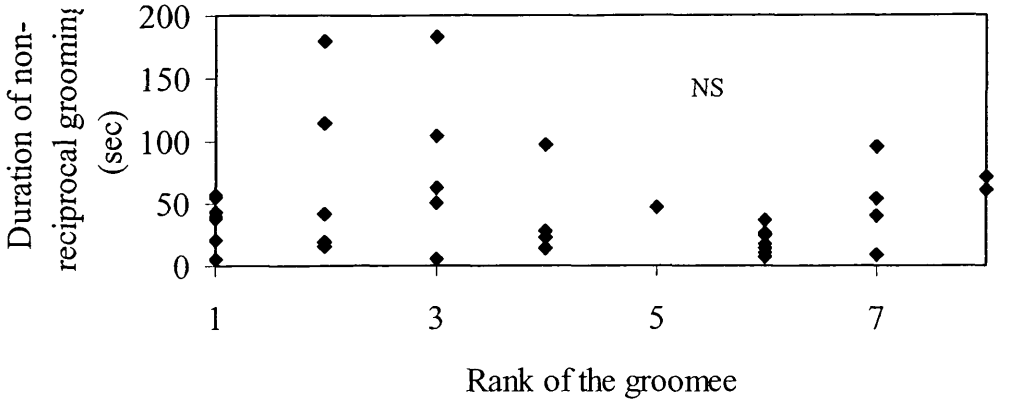


Figure 4.5: Relation between the duration of non-reciprocal grooming (seconds) and the rank of the groomee.



Prediction 5: The degree of grooming reciprocation will be negatively correlated with the rank distance of the partners.

Method A (dyads).

I correlated the differences in the duration of immediately reciprocated grooming bouts (duration of second episode minus duration of first episode), which measured the degree of grooming reciprocation, and the difference in the ranks of the two females (rank of the female that groomed second minus rank of the female that groomed first). This correlation was significant ($r_S = 0.371$, N = 44, $p < 0.01$) even when dyads consisting of kin individuals were left out ($r_S = 0.374$, N = 40, $p < 0.01$). However, the differences in the interactants' rank and of the episodes' duration were both negative when higher-ranking females were the first to perform the service, because they groomed less. On the contrary, positive differences in both variables occurred when the groomers starting the affiliative interaction were lower-ranking females. Therefore, it was more reliable to verify whether degree of reciprocation decreased with increasing rank distance using the variables' absolute (unsigned) differences. This correlation was not significant either when all selected dyads were included in the analysis ($r_S = 0.075$, N = 44,

NS; Figure 4.6) or when dyads composed by kin females were excluded (r_S = 0.026, N = 40, NS).

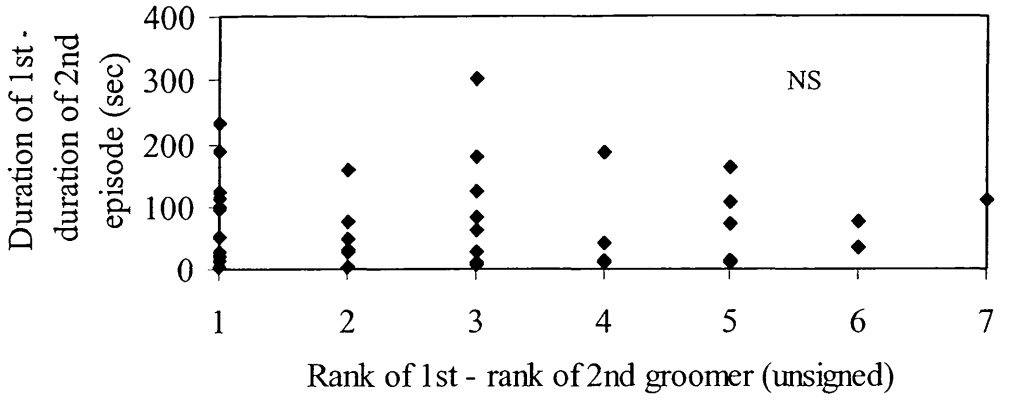
Method B (matrix).

In order to analyse the relationship between the degree of grooming reciprocation and the rank distance of the grooming partner, a matrix with the difference of grooming given and received was created (appendix B.3A). Moreover, a matrix containing the rank distances of groomers and groomees was created (appendix B.4a). A row-wise correlation between these two matrices gave a non-significant result (Tau_{rw} = 0.226, NS). This result remained basically unchanged when the effect of kinship was partialled out ($Tau_{rw,xy,z}$ = 0.224; NS). By the same reasoning used above, it is more reliable to analyse the relation between degree of grooming reciprocation and rank distance using unsigned matrices (de Vries, 1993). Therefore, the same analyses were rerun using a matrix with the unsigned difference of grooming given and received and a matrix with the unsigned rank distances of groomers and groomees. The test showed a non-significant tendency of partners far away in rank to reciprocate grooming less than those of adjacent rank (Tau_{rw} = - 0.234, p = 0.070). When the effect of kinship was partialled out, there was no inverse relation between rank distance of grooming partners and degree of reciprocation ($Tau_{rw,xy,z}$ = - 0.131; NS). Therefore, the non-significant tendency found above was due to the confounding influence of kinship, as related females generally share similar ranks in the Japanese macaques (see Chapter 1).

Interpretation.

Neither the analyses based on dyads nor those based on matrices supported Prediction 5.

Figure 4.6: Relation between the unsigned degree of grooming reciprocation (seconds) and the unsigned rank distance between grooming partners.



Prediction 6: Females will devote an equal amount of reciprocal grooming to distantly and to closely ranking partners but they will give more non-reciprocal grooming to distantly ranking partners.

Method A (dyads).

Based on the considerations discussed for prediction 5 (see above), I only used the unsigned rank distance between grooming partners to test prediction 6. Following this procedure, reciprocal grooming was not related to the unsigned rank distance between the grooming partners when using dyadic scores (r_S = -0.166, N = 44, NS; Figure 4.7). However, in conflict with the prediction, non-reciprocal grooming was also not related to rank distance (r_S = -0.119, N = 35, NS; Figure 4.8). When dyads of kin females were excluded, the significance of the previous correlations did not change either for reciprocal grooming (r_S = -.0063, N = 40, NS) or for non-reciprocal grooming (r_S = 0.244, N = 31, NS).

Method B (matrix).

I correlated a matrix containing the overall reciprocal grooming (Appendix B.1) and those containing the unsigned rank distance between the grooming partners. There was an inverse relation between reciprocal grooming and rank

distance (Tau_{rw} = - 0.372, $p < 0.01$). When the effect of kinship was partialled out the significance of the relation did not change ($Tau_{rw,xy,z}$ = - 0.278, $p < 0.05$). Similarly, a greater amount of non-reciprocal grooming was exchanged between closely ranking females than between distantly ranking females (Tau_{rw} = - 0.317, $p < 0.05$). Partialling out the effect of kinship, the above trend remained, even though the coefficient did not reach statistical significance ($Tau_{rw,xy,z}$ = - 0.215, $p = 0.068$).

Interpretation.

The analyses run using dyadic scores supported the first part of this prediction (i.e. reciprocal grooming was not affected by rank distance) but not the second (i.e. non-reciprocal grooming was not directed more to distantly ranking females). Moreover, matrix correlations did not support both these predictions.

Figure 4.7: Relation between the duration of reciprocal grooming (seconds) and the unsigned rank distance between the grooming partners.

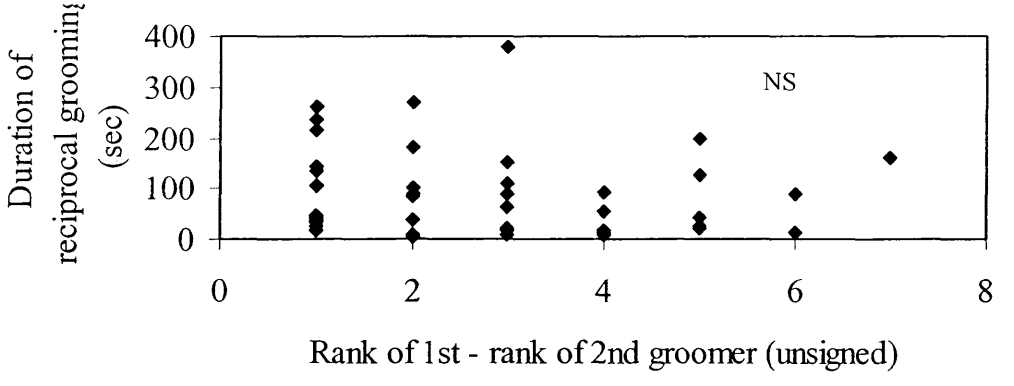
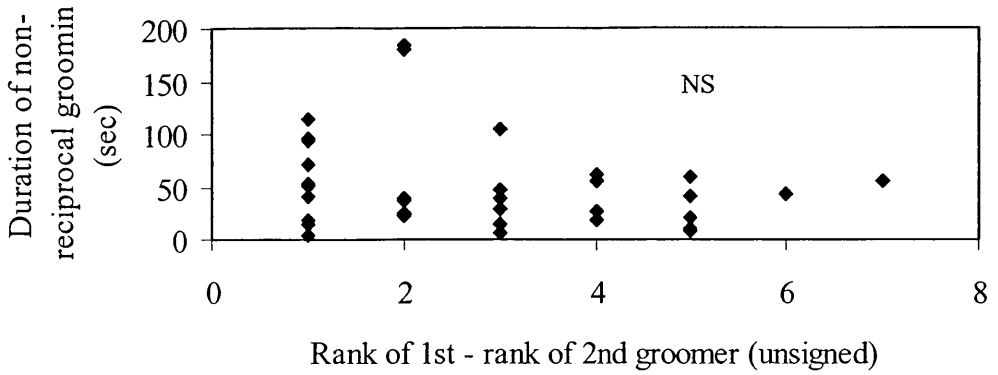


Figure 4.8: Relation between the duration of non-reciprocal grooming (seconds) and the unsigned rank distance between the grooming partners.



4.4 Discussion.

In the present work two different analytical approaches were used, one performing investigations at dyadic level and using immediately reciprocated against non-reciprocated grooming, and the other running tests at group level on total grooming exchanged. They gave contrasting results regarding the distribution of grooming (see Table 4.2). When analysing immediately reciprocated grooming within dyads (Barrett *et al.*, 1999), it appeared that female Japanese macaques in Yakushima did not match time contributions. On the other hand, row-wise matrix correlation revealed that, overall, the longer a female spent grooming a group mate, the longer her partner groomed her in return. That is, overall grooming was reciprocated. No correlation run at the dyadic level showed any rank-related benefit associated with the performance of grooming. For example, within each reciprocated grooming episode, the difference between distantly ranking partners' time contributions was not greater than that between closely ranking partners, contradicting Barrett and colleagues' (1999) predictions. Conversely, matrix correlations partly supported this picture as both total grooming and non-reciprocal grooming were mainly directed up the hierarchy. These results suggest the potential of interchange trading of grooming among

female macaques in Yakushima, as expected according to the biological market theory in species characterised by strict dominance relationships. The effect of various factors on grooming distribution and its interchange for other goods will be extensively analysed in the next three Chapters.

Table 4.2: Summary table of the predictions tested in this Chapter with the two methodologies and in relation to kinship (dyads: analyses run using Spearman rank correlation; matrices: analyses run using row-wise Kr-test).

Prediction	Method			
	Dyads		Matrices	
	Including kin	Excluding kin	Including kin	Partialling-out kin
1: Grooming will be directed more up than down the hierarchy.	-	-	Yes	Yes
2: Grooming given and received will be positively correlated.	-	-	Yes	Yes
3: Reciprocal and non-reciprocal grooming will have different allocation.	Yes	Yes	-	-
4.1: High-ranking females will receive as much reciprocal grooming as low-ranking females.	Yes	Yes	Yes	-
4.2: More non-reciprocal grooming will be directed up than down the hierarchy.	-	-	Yes	Yes
5: The degree of grooming reciprocation will be negatively correlated with the rank distance of the partners.	-	-	Almost significant ($p = 0.070$)	-

6.1: Females will devote an equal amount of reciprocal grooming to distantly and to closely ranking partners.	Yes	Yes	-	-
6.2: Females will give more non-reciprocal grooming to distantly ranking partners.	-	-	-	-

The main aim of this Chapter was to determine which method could more reliably test grooming distribution in Yakushima macaques. By comparing the two different methods that have been most often used to study grooming relationships in primates, I aimed to justify the use of a single method in the following Chapters where the effect of various factors on grooming distribution will be specifically analysed. It is worth stressing here the importance of using only one method for the following Chapters. It would have been possible to use both approaches for every analysis run, but it is clear that this would also have created confusion on how to interpret the results. Given that the two statistical approaches consistently gave discrepant results in this Chapter, it is very likely that this would happen for many other analyses. This is the case, for example, when different indices to measure reproductive skew are employed using the same data set (e.g. Kokko *et al.*, 1999). In such a situation, it is more effective to choose the analytical approach that better fits the data available, bearing in mind that alternative methodologies may bring different results.

To avoid the confusion created by having different results with different analytical approaches, it was decided that only matrix correlation with overall grooming exchanged between two females will be used in the following Chapters for analysing the factors affecting grooming distribution. This decision is based on three considerations. First, from the methodological point of view, there are clear advantages of studying reciprocity and other social interactions at a group level rather than at a dyadic level (Hemelrijk, 1990). Analyses run at the group level and using matrices do not inflate the sample size whereas this happens for analyses run at the dyadic level. This problem is not avoided when only one social interaction is used for each dyad, as Barrett and colleagues did (Barrett *et*

al., 1999). For example, the sample size for the Spearman rank correlations run in this Chapter ranged between 44 and 35 (see above) even though I randomly selected only one grooming bout per dyad. This figure is significantly larger than the actual number of females in Nina A group (N = 8) which represents the true sample size for this study. Moreover, analyses based on randomly selected dyads have been criticised (Hemelrijk, 1990; see also Aureli and van Shaik, 1991; de Waal and van Roosmalen, 1979) because the sample obtained may not be representative of the original one, whatever the procedure used for selecting dyads is.

Second, from a practical point of view, the decision to collect focal observations lasting only 10 minutes (see Chapter 2 for the reason behind this decision) significantly reduced the number of grooming interactions between two females that were observed from the start to the end (i.e. 29.3% of total grooming interactions observed). This means that a small proportion of grooming observed could be considered as immediately reciprocated (i.e. 17.9 %) or non-reciprocated (i.e. 11.4 %), according to the definition from Barrett and colleagues (1999). Therefore, data on grooming immediately reciprocated or not reciprocated were significantly biased, making it very difficult to draw reliable conclusions from the analyses performed. In this view, much more reliable are the analyses run on total grooming exchanged between two females and using matrix correlations, as all grooming interactions observed are used.

Third, from a theoretical point of view, analyses on immediately reciprocated and non-reciprocated grooming may not effectively address grooming reciprocation and interchange in primates. Indeed, my colleagues and I (Schino *et al.*, 2003) have recently proposed that pitting immediately reciprocated against non-reciprocated grooming bouts is not an appropriate method to identify and distinguish reciprocal from interchange traders (see Section 4.1 above). It seems unlikely that remembering the duration of each single grooming bout is so important for mammals characterised by complex cognitive capacities and forming stable social groups, such as the Japanese macaques (Cheney and Seyfarth, 1990b). They seem rather to rely on keeping in mind and balancing overall benefits given and received during periods of relatively constant

ecological conditions in order to maintain inter-individual relationships that are advantageous as long as those particular circumstances last (Schino *et al.*, 2003). Moreover, it has been argued that since long-term social relationships are an emergent property of short-term interactions, a distinction between the two is artificial (Cords and Aureli, 1996; de Waal and Tyack, 2003). In conclusion, independent criteria rather than temporal patterning are needed to recognise trader classes in order to test the occurrence of grooming reciprocation and interchange (Henzi and Barrett, 2002).

The biological market approach is principally concerned with the manner in which individual behaviour reflects changes in the market place and the supply and demand of valuable commodities. However, the data used in the present work were based on overall outcomes rather than on particular individual interactions. Hence, they only put in evidence a trend in line with biological market expectations, but did not really test for the impact of market forces. For this reason, in the following chapter further investigations will be performed. Different ecological conditions will be compared, in order to verify whether the study females effectively traded grooming for other goods, increasing the price paid with the group mates' social status.

CHAPTER 5

SEASONAL CHANGES IN THE DEGREE OF GROOMING RECIPROCITY

In Chapter 4 I argued that grooming distribution in Japanese macaques is more reliably analysed using row-wise matrix correlations than using dyads. Matrix correlation will be thus used in this Chapter (and in the rest of the Thesis, whenever appropriate) in order to analyse if and how seasonal changes in activity budgets and diet composition affect grooming distribution and reciprocation. The eight females living in Nina A group were the subjects of this study as they were the only monkeys for whom data were collected throughout the year (data on Kw females were only collected for approximately 4 months; see Chapter 2).

5.1 Introduction.

Social animals often have to cope with short- and/or long-term variations in resource abundance and thus in the level of competition for those resources. The harshness of the competitive regime may influence the nature of social relationships among group members so much that it can shape the structure of female-bonded groups (e.g. van Schaik, 1989; see Chapter 1). Female social systems may be labelled "egalitarian" when the steepness of the dominance hierarchy is shallow, or "despotic", when social rank is associated with elevated power differential in withholding access to monopolisable resources among group mates (van Schaik, 1989; 1996; van Hooff and van Schaik, 1992; Vehrecamp 1983). Egalitarian social systems are expected in species or populations facing a low level of within-group contest food competition while despotic species should be usually characterised by a high level of contest food competition (see Chapter 1 for a discussion of the rationale behind this hypothesis). The biological market theory is one of the principles proposed to explain changing patterns of social

relationships within a number of species that may be "strategic" responses to local ecological circumstances and to current balances of power (Barrett *et al.*, 1999; Barrett and Henzi, 2001; Cords, 2001; Manson *et al.*, 1999; Noë, 1990; Silk *et al.*, 1999; Stopka and MacDonald, 1999). In other words, the theory predicts that the social relationships between group members (measured in terms of grooming exchange and aggressive interactions; see Chapter 1) will change in terms of their quality (i.e. amicable or agonistic) and symmetry (i.e. the "commitment" of each monkey to a given relationship) according to the ecological context. Indeed, fluctuation of resources in the habitat can be compared to the changing supply and demand of "valuable commodities" in human market places, and social animals can be considered as traders of these precious goods (e.g. agonistic support, grooming, tolerance at food sites: see Chapter 1). The biological market theory explicitly builds in the notion of "partner choice", which is a key feature of primate societies (Barrett and Henzi, 2001). In primate groups, where animals may have many potential partners from whom to choose, trade should be determined by their standing in the market-place and the goods which they can offer. Power differentials, or resource holding potential (RHP), among individuals can be expressed in terms of the distance between the individuals' respective dominance ranks (Henzi and Barrett, 1999). When resources are abundant and/or not monopolisable by dominant monkeys, agonistic interactions between group members should be rare and within-group competition low. In such an ecological context, according to the biological market theory, grooming should be mainly exchanged for itself. That is, reciprocal traders of grooming will prevail and the effect of rank distance on grooming distribution and reciprocation is expected to be weak. When, however, resources are scarce and/or clumped, preferential access to those resources by dominant animals should appear, agonistic interactions should become frequent and contest food competition should be high. Under these circumstances, grooming should mainly be directed up the hierarchy and should become less reciprocated as subordinates may use it to buy other commodities (i.e. tolerance or access over resources; see Chapter 1). Reciprocal trading will still be found among individuals with a similar RHP (Barrett *et al.*, 1999).

To date the only direct test of the Biological Market theory central assumptions was given by Barrett *et al.* (2002) and Henzi and Barrett (2002) in female chacma baboons (*Papio cynocephalus ursinus*). In those studies patterns of grooming in relation to tolerance around food sites and access to infants showed evidence for interchange: grooming was less reciprocated when subordinates had to "buy" these other commodities. Along with colleagues, I have recently investigated (Schino *et al.*, 2003) the occurrence of grooming reciprocation and interchange in captive female Japanese macaques. We showed that, in this species, grooming was directed up the hierarchy and, thus, probably interchanged with other rank-related benefits. In captive groups, social relationships reflect an equilibrium state (Chapais *et al.*, 1995) and hence this is not the ideal setting to test for the impact of market forces, unless one varies local circumstances. On the contrary, in natural conditions ecological changes may be detected, making this investigation more appropriate. Majolo (2004), working in Yakushima during the year of this study, found that the peak of fruits and seeds production, and consequently of consumption by the monkeys, occurred in July-August, whereas the highest level of leaf consumption took place in February-April (see also Hill, 1997; Maruhashi, 1980; Nakagawa, 1989, 1990; Nakagawa *et al.*, 1997; Noma, 1997). For a given amount of food, fruits and seeds give an animal a higher net energetic gain than leaves (Dunbar, 1988; Stephens and Krebs, 1986), consequently competition is expected to arise when fruits and seeds are limited. Indeed, Majolo (2004) reported that conflicts over food approximately doubled during February-April in comparison to July-August. Moreover, monkeys spent significantly less time foraging and moving in the period July-August than in the period February-April. This was probably due to the fact that the monkeys fulfilled their daily energetic requirement quicker when foraging on fruits and seeds. Hence, in Yakushima it was possible to identify two periods of differential availability of high energetic foods. As a consequence of this, it is possible that changes in time spent searching for food affect the time available for grooming exchange and thus the type and quality of social interactions among group members (e.g. Janson and Chapman, 1999; Mc Farland Symington, 1988; Pruetz and Isbell, 2000; Sterck *et al.*, 1997). Therefore, the first aim of this Chapter was

to investigate whether seasonal variation in fruit and seed availability had any effect on the time that females spent grooming as well as on grooming distribution among partners. Moreover, the "value" of dominant females is expected to be higher in periods of high food competition than when competition is low, as the benefits for subordinate animals of obtaining tolerance near food are higher in the former than in the latter condition. If this is so and if grooming is indeed exchanged for other commodities (see Chapter 7), one may expect to see less reciprocal grooming when food competition is high than when it is low for animals who have a more urgent need to "buy" other commodities (i.e. tolerance near food sources) in the former situation. Therefore, the second aim of this study was to evaluate whether, and to what extent, females reciprocated grooming in both July-August and February-April. In particular, the following specific predictions were tested, in order to verify the occurrence of interchange between grooming and tolerance near fruit-seed sites:

1) Females should direct more grooming up the hierarchy in February-April when food competition was highest, whereas the distribution of this affiliative behaviour should be less dependent on the recipient's rank in July-August. Females are expected to trade grooming for other grooming and, at the same time, for tolerance around food sites. For this reason there should also be a negative correlation between the groomees' rank and the difference between grooming given and received by those individuals in February-April. This finding would suggest that in this period higher ranking females received more grooming than they gave to lower ranking partners. This relation should be weaker or absent in July-August.
2) All females are able to trade reciprocally and are assumed to need grooming. Thus, most grooming should take place between closely ranked females in both periods. However, in February-April this tendency should be weaker as females will try to interact more with distantly (higher) ranking partners in order to interchange grooming with tolerance near fruit-seed sites.

3) There should be a positive correlation between grooming given and received in both periods. However, in February-April the strength of reciprocation should be weaker than in July-August, when there was a lower competition for fruits and seeds, suggesting that a certain proportion of grooming time was exchanged for tolerance around fruit-seed sites in this period.

The time that birds and mammals spend looking for food is often considered to be a reliable measure of food availability (Norberg, 1977; Pyke *et al.*, 1977). Studies on primates have shown that this is also true for the Japanese macaques on Yakushima (Agetsuma, 1995) as well as for other species (e.g. green monkeys, *Cercopithecus sabaeus*: Harrison, 1985; titi monkeys, *Callicebus personatus melanochir*: Heiduck, 2002). Monthly analyses on time spent foraging, level of aggression over food, and grooming distribution will be used to test the above predictions (along with the comparisons of the two time periods). It should be found that the more time the females spend foraging for fruits and seeds (indicating high food abundance), the lesser is their tendency to direct grooming up the hierarchy (prediction 1) and their preference for distantly ranking grooming partners (prediction 2), but stronger is their readiness to reciprocate grooming (prediction 3). The opposite trend should appear the higher the rate of aggression over food.

5.2 Methods.

a) Study subjects and data collection.

All eight full-adult and sub-adult females belonging to Nina A troop were subjects of this investigation (as for Kw females, data were not available for the whole study year).

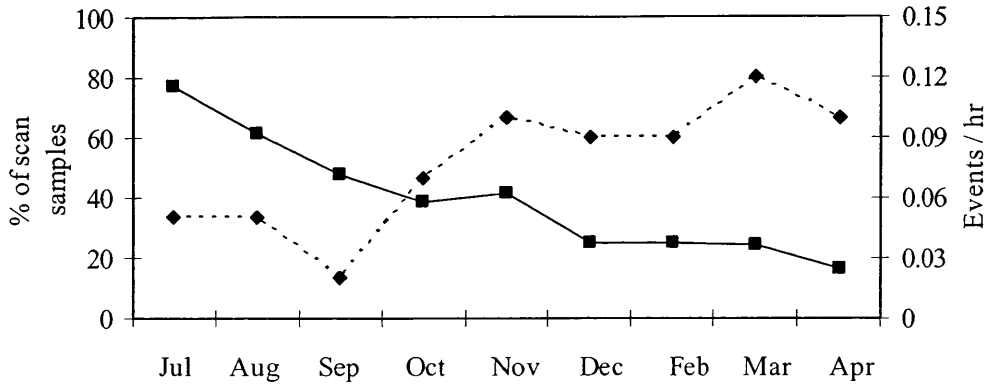
In order to analyse how grooming distribution varied throughout the year I followed two analytical approaches. First, I compared grooming distribution in two periods (i.e. July-August 2001 and February-April 2002) that a parallel study showed to differ in fruits-seeds availability (Majolo, 2004). For the period from

July to August 2001, 43.2 hrs of focal observation were collected (5.4 ± 0.2 mean hrs of observation per female ± SE) and for the period from February to April 2002 58.5 hrs were collected (7.3 ± 0.2 hrs per female). These two periods occurred in the non-mating season as during the course of this study the mating season started the 28th August and ended in late December 2001 (see Hanby and Brown, 1974 for a definition of mating season). By analysing two periods with different food availability and both in the non-mating season, any effect of sexual activity on grooming distribution and competition (a potentially confounding variable: D'Amato *et al.*, 1982; Mehlman and Chapais, 1988) was ruled out. Second, data recorded throughout the year of this study (June 2001- April 2002, Chapter 2) were used to run monthly correlations between time spent foraging for fruits and seeds and grooming distribution. By running these correlations I aimed to determine if monthly variations in activity budgets and/or food competition had any immediate effect on grooming distribution.

I built up a linear dominance hierarchy for the group based on the outcome of decided agonistic encounters between females and on the direction of spontaneous submissive acts recorded either *ad libitum* or during focal animal sampling (Chapter 2). Data on the duration of grooming were collected during focal animal sampling in order to calculate proportions of time the females spent performing this affiliative behaviour (Altmann, 1974; Martin and Bateson, 1993).

Data on time spent foraging for fruits and seeds by the females and on frequency of aggression over food are taken from Majolo (2004; see Figure 5.1).

Figure 5.1: Monthly percentage of time spent foraging on fruits and seeds (continuous line; % of scan samples) and monthly frequency (events / hr) of conflicts over food (dashed line; redrawn from Majolo, 2004)



b) Data analysis.

I used the Shannon-Wiener diversity index in order to compare females' grooming allocation in the two periods. This index has been elaborated for communication theory studies (Shannon and Wiener, 1949) but it is also currently employed in population biology, in ecology (Wilson and Bossert, 1971) and in social behaviour (Cheney, 1992; Henzi *et al.*, 1997; Nakamichi and Shizawa 2003; Watts, 2000). The diversity index H is computed by the formula:

$$H = - \Sigma p_i (ln\ p_i)$$

where p_i is the proportion of grooming given to the i^{th} individual (i.e. ratio of the grooming given to individual i^{th} to total grooming given). The hypothetical maximum diversity index is obtained by the formula (Henzi *et al.*, 1997):

$$H_{max} = ln\ N$$

where N is the number of potential grooming partners of each individual in a group (N = 7 for Nina A). A grooming diversity ratio (DGR; Cheney, 1992; Di Bitetti, 2000) is given dividing the actual diversity index (H_s) of each individual by the theoretical maximum diversity for a group of a given size. This is the measure that I used to determine how evenly female macaques distributed

grooming among their potential partners. If a female grooms all the potential partners about equally (see also Table 1.1 for my definition of grooming equality) her DGR approaches 1, while her DGR is considerably less than 1 if she grooms only some potential partners or grooms some individuals considerably more than others. The use of Shannon-Wiener index in estimating grooming distribution has been criticised on the ground that it does not control for group size and for discrepancy in sampling effort (Di Bitetti, 2000). Differences in sampling effort may potentially affect the number of grooming partners per female and grooming distribution. To control for this possibility, I correlated the sampling effort for each subject and the number of her grooming partners in July-August and in February-April. It appeared that sampling effort did not influence females' grooming allocation (Spearman correlation: July-August: $r_S = -0.66$, N = 8, NS; February-April: $r_S = -0.13$, N = 8, NS). Moreover, sampling effort was evenly distributed towards all the study animals (see Chapter 2). These two results, together with previous studies using this index (e.g. Henzi *et al.*, 1997) support the use of the Shannon-Wiener index as a reliable measure of grooming inequality.

Row-wise matrix correlation was used to test for preference for high ranking and close-ranking individuals as grooming partners in July-August and February-April. Row-wise matrix correlation was also used to analyse grooming reciprocity and the relation between the degree of time matching and rank distance between groomers and groomees in the two time periods (Hemelrijk, 1990; de Vries, 1993; see Chapter 4). The proportion of time that each female spent grooming all the partners was calculated in July-August and February-April and entered in the matrices. Matrices with individuals' rank and rank distance between each dyad were employed (see Chapter 4).

I also ran Kr tests using matrices with the percentage of total grooming given by the female macaques in July, August, September, October, November, December, February, March, April. Tau-values obtained correlating this matrix and its transposition (grooming received) were used to evaluate the monthly degree of grooming reciprocation. Tau-values obtained correlating the matrix of grooming given with the matrix of the groomees' rank and with the matrix of the

unsigned rank difference between groomers and the groomees were employed as indices of the monthly tendency to groom dominant females and closely ranking females, respectively.

5.3 Results.

a) Overall grooming distribution in July-August and in February-April.

The percentage of time spent grooming was higher in July-August than in February-April (Wilcoxon test: $T = 37$, $N = 8$, $p < 0.05$; Figure 5.2). Females groomed the same number of individuals in the two periods ($T = 9.0$, $N = 8$, NS; Figure 5.3). Furthermore, a comparison of the Shannon-Wiener index showed that the way in which females directed grooming towards their partners did not change between July-August and February-April ($T = 22.0$, $N = 8$, NS; Figure 5.4).

Figure: 5.2: Percentage of time spent grooming by Nina A females in the two study periods (N = 8; mean percentage ± SE).

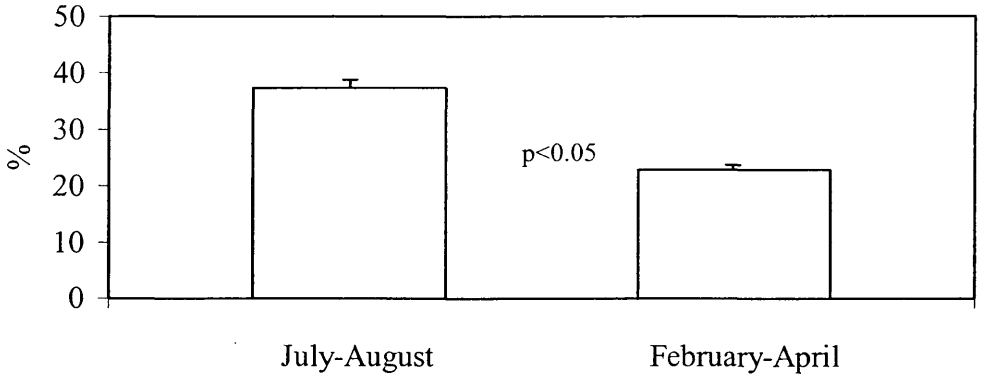


Figure 5.3: Number of grooming partners for Nina A females in the two study periods (N = 8; mean number of female partners ± SE).

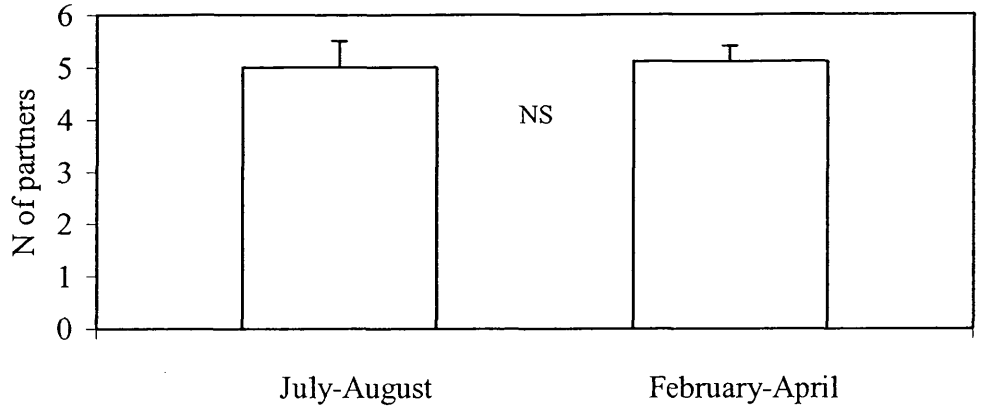
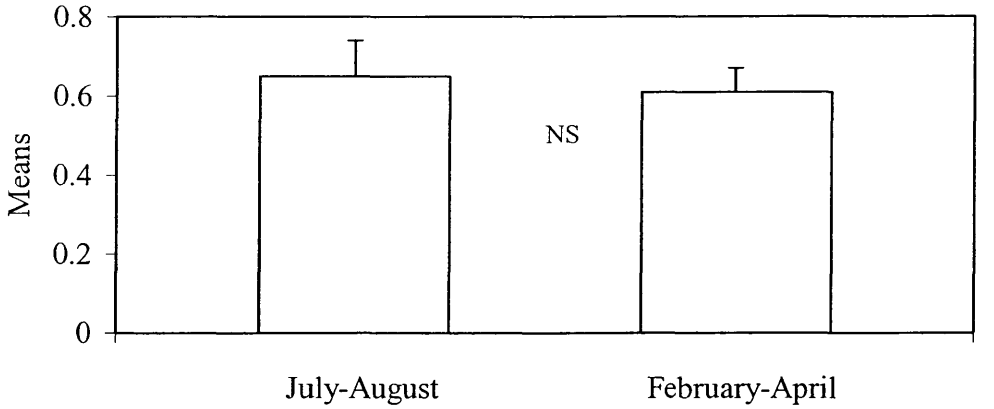


Figure 5.4: Shannon-Wiener diversity index for Nina A females in the two study periods (N = 8; mean grooming diversity ratio ± SE).



b) Seasonal variation in the balance between grooming reciprocation and interchange.

Prediction 1

Female Japanese macaques did allocate a greater amount of grooming to higher-ranking partners than to lower-ranking ones in February-April (Row-wise matrix correlation: $Tau_{rw} = - 0.243$, $p < 0.015$; Appendix B.5 and Table 4.1b). When the effect of kinship was partialled out the above trend became much stronger ($Tau_{rw,xy,z} = - 0.350$, $p < 0.0003$). However, this relation was not significant in July-August ($Tau_{rw} = - 0.114$, NS; Appendix B.6 and Table 4.1b), even when related individuals were left out from the correlation ($Tau_{rw,xy,z} = - 0.195$, NS), supporting Prediction 1.

I correlated the differences in the duration of grooming (duration of grooming given minus duration of grooming received) and the ranks of the receiving partners (Appendix B.7 and B.8, and Table 4.1b). This correlation was significant in July-August ($Tau_{rw} = - 0.369$, $p < 0.038$), even when kin were partialled out ($Tau_{rw,xy,z} = - 0.359$, $p < 0.040$), but not in February-April ($Tau_{rw} = - 0.187$, NS; excluding kin: $Tau_{rw,xy,z} = - 0.184$, NS). These results contradicted prediction 1. Indeed, high-ranking females received more grooming than they gave when high-energetic food was abundant and there was less competition for it, where such tendency did not emerge in the other food-availability condition.

I considered the Tau-values obtained from the row-wise matrix correlations between grooming given by each subject and rank of the receiving female in July, August, September, October, November, December, February, March, April, as a clue to any preference for high ranking individuals as grooming partners in each month. A Spearman correlation between these Tau-values and the proportion of time the female macaques fed on fruits and seeds showed no tendency to direct grooming up the hierarchy when there was lower fruit and seed availability ($r_s = 0.20$, $N = 9$, NS; Figure 5.5). Correlating again the Tau-values, index of the inclination to direct grooming up the hierarchy with the aggression rate over food in each month, it emerged that females did not tend to show more affiliative

behaviours towards higher ranking partners when food competition increased (r_s = -0.28, N = 9, NS; Figure 5.6).

Figure 5.5: Scatter-plot (N = 9) of the relation between monthly percentage of time spent foraging on fruits and seeds and the tau values of the matrix correlations between grooming given and rank of the groomee for Nina A females.

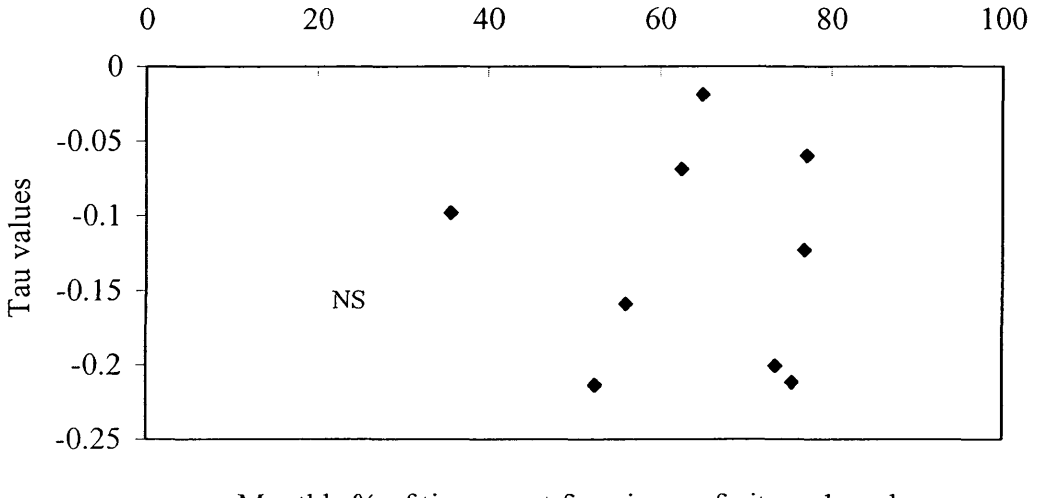
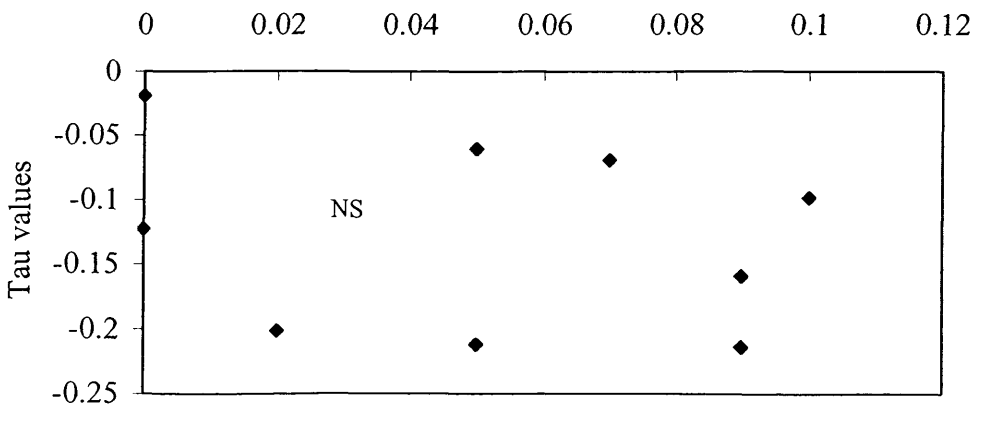


Figure 5.6: Scatter-plot (N = 9) of the relation between monthly rate of aggression over food and the tau values of the matrix correlations between grooming given and rank of the groomee for Nina A females.



Prediction 2

Females tended to groom closely-ranking group mates more than distantly ranking ones both in February-April ($Tau_{rw} = - 0.354$, $p < 0.009$) and in July-August ($Tau_{rw} = - 0.268$, $p < 0.041$), as indicated by the negative relation between grooming given by each individual to all the partners (Appendix B.5 and B.6) and the unsigned difference between groomers and groomees' rank in these periods. Excluding kin did not substantially change the result of the analysis in February-April ($Tau_{rw,xy,z} = - 0.255$, $p < 0.047$), although the correlation became non-significant in July-August ($Tau_{rw,xy,z} = - 0.168$, NS). According to Prediction 2 the opposite result should have been found.

I used the Tau-values obtained from the row-wise matrix correlation between grooming given by the study females and the absolute difference between the groomers' and the groomees' rank in July, August, September, October, November, December, February, March, April, as an index of the tendency to direct grooming to partners occupying distant positions in the hierarchy in each month. Then I correlated these values with the proportion of time spent eating fruits and seeds in each month, in order to analyse the females' preference for closely ranking partners in different condition of fruit and seed abundance. Grooming distribution between closely and distantly ranking females was unaffected by monthly variations in time spent foraging for fruits and seeds ($r_S = - 0.117$, $N = 9$, NS; Figure 5.7). In addition, the Tau-values, indicating the females' tendency to groom group mates far away in rank, were not correlated with the rate of aggression over food in each month, confirming that the tendency to groom closely ranking females did not vary in different competitive regimes ($r_S = 0.093$, $N = 9$, NS; Figure 5.8).

Figure 5.7: Scatter-plot (N = 9) of the relation between monthly percentage of time spent foraging on fruits and seeds and the tau values of the matrix correlations between grooming given and absolute rank distance of Nina A females.

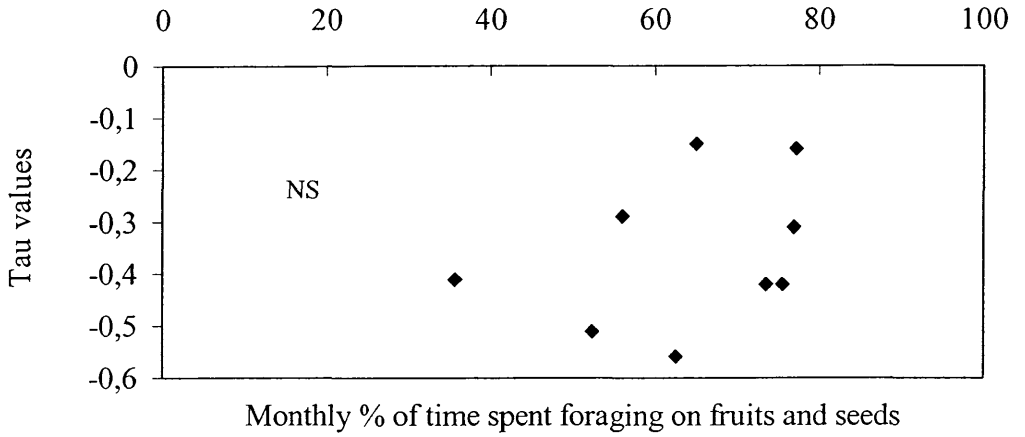
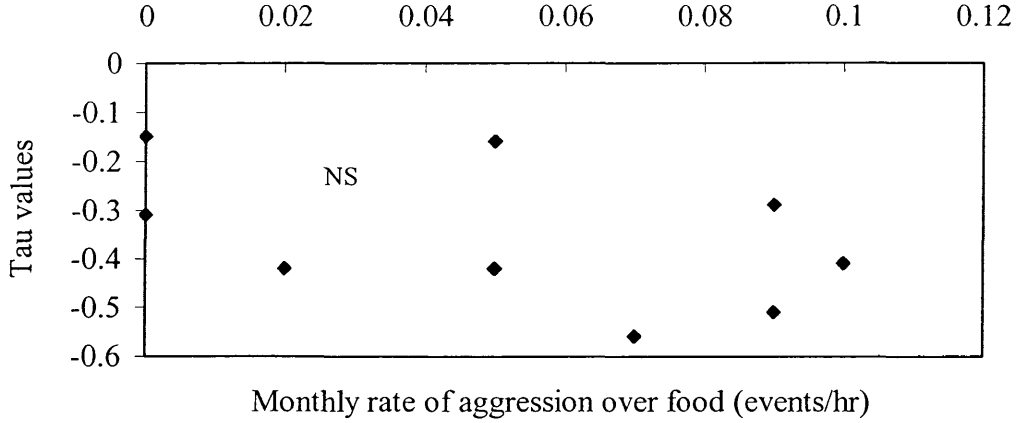


Figure 5.8: Scatter-plot (N = 9) of the relation between monthly rate of aggression over food and the tau values of the matrix correlations between grooming given and absolute rank of Nina A females.



Prediction 3

A row-wise matrix correlation between the matrix of total grooming given (Appendix B.5 and B.6) and its transposed matrix revealed that females did reciprocate the amount of grooming they received in July-August ($Tau_{rw} = 0.348$, $p < 0.0033$) and in February-April ($Tau_{rw} = 0.529$, $p < 0.0001$). Partialling out the effect of kinship did not alter the direction of the correlation, although the significance was reduced (July-August: $Tau_{rw,xy,z} = 0.256$, $p < 0.0239$; February-April: $Tau_{rw,xy,z} = 0.446$, $p < 0.0004$). However, the correlation was much stronger in February-April when there were more conflicts over food and less fruit and seed availability than in July-August, contrasting with prediction 3.

I used the Tau-values obtained from the row-wise matrix correlation between grooming and being groomed in July, August, September, October, November, December, February, March, April, as an index of the tendency to reciprocate grooming in each month. Then I correlated these values with the proportion of time spent eating fruits and seeds in each month, in order to investigate the females' tendency to return the amount of grooming received in different condition of fruit-seed abundance. There was no significant relation between the two variables ($r_S = - 0.467$, $N = 9$, NS; Figure 5.9). Similarly, no significant correlation appeared between the Tau-values, a sign of the females' eagerness to reciprocate grooming and the rate of aggression in each month, showing that grooming time matching did not vary in different competitive regimes ($r_S = 0.000$, $N = 9$, NS; Figure 5.10).

Figure 5.9: Scatter-plot (N = 9) of the relation between monthly percentage of time spent foraging on fruits and seeds and the tau values of the matrix correlations between grooming given and received from Nina A females.

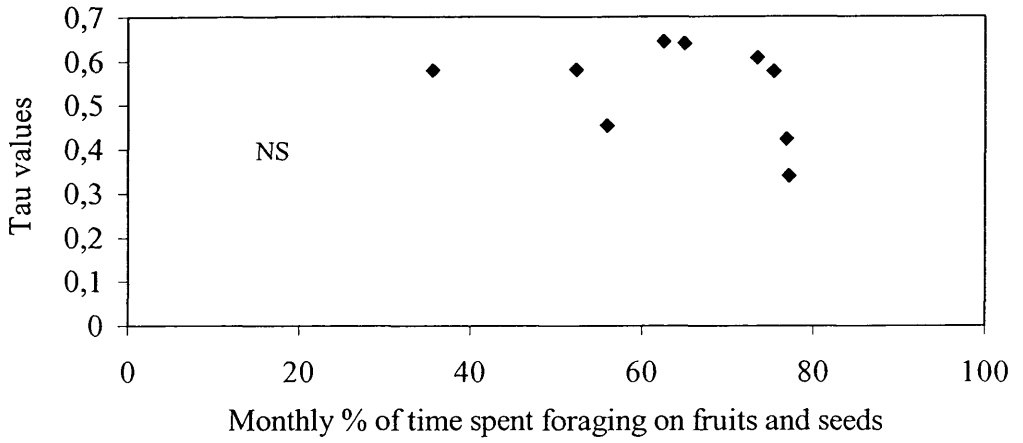
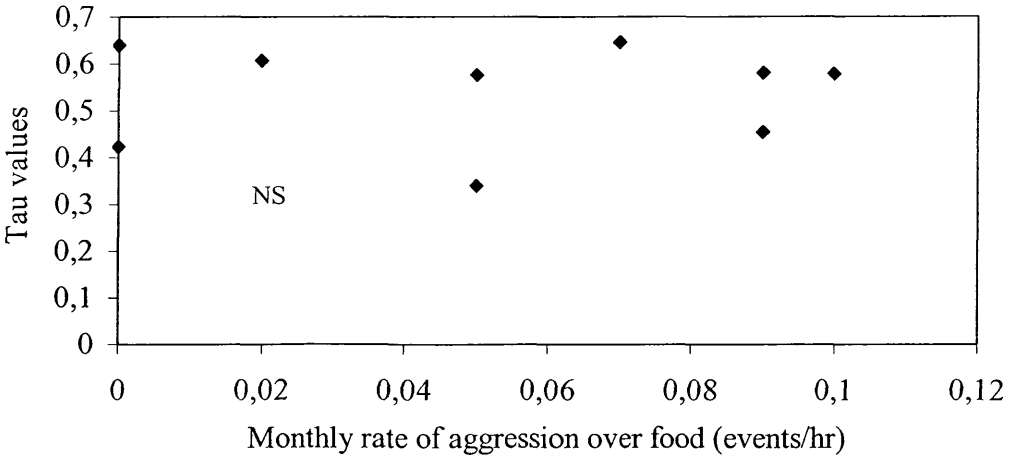


Figure 5.10: Scatter-plot (N = 9) of the relation between monthly rate of aggression over food and the tau values of the matrix correlations between grooming given and received from the females.



5.4 Discussion.

Before specifically discussing the various results of this Chapter, it is important to notice one thing. In this study, evidence of the possible exchange of grooming for other benefits was only indirect. That is, it was only obtained by analysing if and how the degree of reciprocated grooming differed in the various months. The reason for this was that a preliminary analysis of the data available showed that observations on the possible benefits of grooming exchange (i.e. tolerance over food sources and agonistic support) were too rare to be analysed on a monthly basis or for the two different periods (i.e. July-August and February-April). Therefore, I decided to analyse if and how grooming gave benefits other than grooming itself, for the whole study period only (see Chapter 7). By doing this, sufficient data were available for statistical analyses but, clearly, the importance of seasonal changes in grooming interchange with other commodities could not be conclusively determined.

a) Overall grooming distribution in July-August and in February-April.

Female Japanese macaques spent significantly more time grooming in July-August than in February-April. In spite of this, the number of grooming partners per female did not increase in July-August and the Shannon-Wiener diversity index revealed no difference in grooming distribution. Although many investigations have demonstrated the influence of food quality and abundance on the activity budgets of social animals and, consequently, on the type and strength of social bonds among group members (Janson and Chapman, 1999; Mc Farland Symington, 1988; Pruetz and Isbell, 2000; Sterck *et al.*, 1997) the results of this study indicated that this was not the case in Yakushima macaques. Majolo (2004) reported that in Yakushima time spent foraging on fruits and seeds never accounted for less than 50 % of total time spent foraging, while time spent foraging on leaves was hardly more than 20 % of total time in February-April. These data suggest that the diet of the female macaques did not change radically throughout the year of this study. Therefore, it may be argued that the increased

foraging behaviour in February-April was due to a different distribution of resources in comparison to July-August, rather than to a significant food scarcity. In winter, females were not forced to dramatically reduce their social activities, which ranged from 37.4 % of time in July-August to 22.4 % of time in February-April. It may be concluded that the difference in time spent grooming, although significant, is not so noticeable as to modify affiliative relationships among the females. Moreover, given the critical role attributed to grooming in recruiting allies, increasing tolerance among individuals, and keeping competition under control (Barrett and Henzi, 2001; Dunbar, 1991; Seyfarth, 1977; see Chapter 7), it is possible that female macaques maintain their grooming network even when they have less time for social activities. Female macaques continued grooming with all partners but less (by a constant proportion) with each, rather than grooming with a few important partners as much as needed to maintain those relationships, thus reducing or avoiding interaction with other usual partners (and increasing inequality of grooming distribution). It has been suggested that the achievement of stable social relations results in social groups showing higher levels of cohesiveness. This should help to establish a coherent team of females, which effectively defend its territory during encounters with neighbouring groups (Rowell *et al.*, 1991) and, in turn, increases females' reproductive success (Pusey and Packer, 1997; van Hooff, 2001). However, this is not a reasonable explanation for the stability of female grooming networks over time in Yakushima. Female macaques rarely take part in inter-group encounters (Majolo *et al.,* 2005; Saito *et al.*, 1998; Sugiura *et al.*, 2000). More likely, the small female cohort size of the study group may have influenced the outcomes of the analyses in this study, even though it mirrored the mean group dimension of Japanese macaques in Yakushima (see Chapter 1). Females belonging to such small social groups may be able to exchange grooming with all other individuals even when time for social activities is shorter. On the other hand, females in large groups with a greater number of potential partners may be forced to reduce the size of their social network during periods of low food abundance. This necessity could result in large social groups becoming less cohesive and, eventually, lead to their fission (Dunbar, 1992; Henzi *et al.*, 1997).

b) Seasonal variation in the balance between grooming reciprocation and interchange.

Since the female macaques of the study group had a clear-cut dominance hierarchy, and food-related agonistic contests occurred, the potential for interchange of grooming and other rank-related benefits existed (see Chapter 7). Indeed, in February-April, when competition for fruit and seed was stronger, females devoted more grooming to higher-ranking partners, whereas this trend did not appear in July-August. However, analysis of monthly data did not confirm this finding as well as all the other results of this study. Female macaques reciprocated most of their grooming in both periods. However, degree of grooming reciprocation was not weaker in periods characterised by high competition for monopolisable resources like fruits or seeds, contrary to what was predicted. Moreover, females directed more grooming to higher ranking partners than they received when there was abundance of high energetic food and less competition for it, rather than vice-versa. According to the biological market theory, females with low-rank distance should always be reciprocal traders, as they are not in the position to trade anything else (they do not differ in resource holding potential). In the study group they were expected to be the preferred partners, as grooming was highly reciprocated in both the periods. However, in February-April higher ranking females should have been the target of interchange grooming for tolerance near food. Consequently, in this period the tendency to allocate more grooming to closely ranking partners should have been weaker than in July-August. Contrary to the predictions, females chose closely ranking individuals as grooming targets more in February-April than in July-August.

It seems that seasonal variations in the level of food competition are too mild to affect the pattern of grooming distribution among the Yakushima female macaques. This may be due to the small group size effect on power differential. In small groups where rank distance can never be very high, the difference between the highest and the lowest ranking females may be insufficient to lead to an interchange relationship (Barrett *et al.*, 1999). Power differential should operate more effectively in larger groups (see Chapter 6).

One other possible explanation for these findings is that there were insufficient market forces operating within the group. In fact, the macaques did not really experience situations of short food supply, at least during the year of data collection (Majolo, 2004). Leinfelder *et al.* (2001) proposed that grooming is not interchanged with another good that, although desirable, does not have its own "equivalent value". It may be that the "value" of grooming was much higher in the Yakushima market place than the "value" of fruits and seeds.

The model proposed by Barrett and colleagues (1999), in which primate groups represent biological markets where individuals exchange grooming for the benefits that it itself offers, as well as for other commodities from more powerful animals, is a promising framework for investigating changing patterns of affiliative behaviour in response to temporary variation in resource availability. However, it may not apply to small social groups and to circumstances in which the value of contested goods does not match the value of grooming.

CHAPTER 6

GROOMING DISTRIBUTION, RECIPROCATION AND PARTNER CHOICE IN A SMALL AND A LARGE GROUP OF FEMALE JAPANESE MACAQUES

I have shown that grooming is relatively unaffected by diurnal changes in ambient temperature and humidity (Chapter 3), and by seasonal changes in activity budgets and level of food competition (Chapter 5). The aims of this Chapter are to analyse how group size affects grooming distribution and reciprocation. All the females living in Nina A group (N = 8) and in Kw group (N = 20) were the subjects of this study.

6.1 Introduction.

The balance between benefits and costs of group living is affected by many ecological and social factors, such as abundance and distribution of food sources, presence of potential predators, and group size (Isbell and Young, 2002; van Schaik *et al.*, 1983; see Chapter 1). It is usually though that social primates establish and maintain long-lasting amicable relationships with some other group members because they may have important consequences on their own fitness (e.g. increased tolerance over food sources; see Chapter 7). Due to these consequences, the evolution of cognitive abilities allowing an animal to maximise the net benefits of social interactions should be favoured (Dunbar, 1988). Indeed, partner choice in grooming interactions depends on the complex interaction of many factors: the resource-holding potential of the social partners (i.e. their capacity to access or monopolise limited resources; see Chapter 5), their willingness to establish amicable relationships though grooming exchange, the presence of genetically-related individuals, the type of social relationships that

other group members have with the potential partners, the level of competition for access to grooming partners, and the time available for social behaviour.

Time is a "hidden" factor that may interact with group size to impose limitations on activity budgets and social "choices" of an animal (Dunbar, 1992; Dunbar and Dunbar, 1988). For example, energy demands associated with lactation and infant transport can eventually cut into grooming time for females (Altmann, 1980; Dunbar and Dunbar, 1988). The need to increase foraging time during periods of food scarcity can also decrease grooming time (Di Bitetti, 1997). Among diurnal animals, such as the Japanese macaques, activities are concentrated during daylight hours (while the reverse is true for nocturnal species). These animals thus have a limited amount of time (which may vary considerably among seasons) to fulfil their daily energetic requirement and to exchange amicable social interactions with the other group mates.

Grooming can indicate the groomer's willingness or need to invest time and effort in a social relationship. For a given time available for social behaviours and other things being equal (e.g. presence of relatives), monkeys may follow two alternative tactics in order to establish or maintain amicable relationships with the other group members: 1) they may exchange grooming with all potential partners as much as possible; 2) they may exchange grooming with a few important partners as much as needed to maintain those relationships and groom with others as much as possible in the time left. Data on male gelada baboons (*Theropithecus gelada*) and male chimpanzees (*Pan troglodytes*) suggest that at least some primates tend to follow this second option (Dunbar, 1984; Watts, 2000). The "choice" between these two possible options also depends on the number of potential partners available. Females living in a relatively small group may groom almost all the available grooming partners even though they do not, or cannot devote a considerable proportion of the day to social behaviour (see Chapter 5). This option, however, becomes more difficult to achieve as the number of potential partners increases. One solution to this problem may be to increase the time for social behaviour at the expense of other, less important activities. For example, baboons living in large groups spend more time grooming than baboons in small groups, by reducing resting time during the day (Dunbar, 1988). It comes

to a point, however, where time for grooming cannot increase any more (unless reducing essential activities such as foraging), and animals are forced to exchange grooming with only some group mates. In such situations, grooming is less evenly distributed among partners and individuals have fewer partners, especially if increased competition (which is usually a by product of increased group size; see Chapter 1) forces individuals to groom key partners disproportionately more in order to maintain alliances.

Henzi and colleagues (1997) showed that, in female baboons, the number of grooming partners for each animal (what they defined as the grooming clique size) and grooming equality varied in relation to group size (see Table 1.1 for my definition of grooming equality). That is, these two variables both increased linearly with increased group size until a certain point (corresponding to a group composed of around 10-12 females). Beyond this group size, the number of grooming partners and grooming equality remained stable or slightly decreased. Henzi and colleagues argued that, in groups larger than around 20 females, female baboons are progressively less able to maintain social relationships with all their potentially valuable partners, so that social cohesion decreases as groups become larger, eventually leading to fission.

It is unclear whether this pattern of grooming distribution is typical only of baboons or if other primates show the same variation in social interactions in relation to group size. Moreover, if grooming equality changes according to group size, the same may happen to partner choice and/or to the degree of grooming reciprocation (see Table 1.1 for a definition). This is because the larger the group, the more animals will attempt to exchange grooming with dominant animals (who have high resource-holding potentials). This should result in a higher level of competition for grooming partners in larger compared to smaller groups. If this is true, grooming reciprocation may be reduced in larger compared to smaller groups as dominant animals are more valuable partners as a consequence of the increased competition. Therefore, subordinate animals in larger groups have to invest more in a grooming interactions with dominant animals (resulting in a reduced degree of reciprocation) than animals of similar rank in a smaller group. In light of these hypotheses, the aims of this Chapter were to analyse the differences between a

larger and a smaller group in relation to: 1) grooming clique size; 2) grooming equality; 3) grooming distribution in relation to the social status of the grooming partners; 4) grooming reciprocation and 5) competition for grooming partners.

As observed by Majolo (2004), studying the same animals as this study, the two groups spent a similar amount of time foraging and moving among food patches. Contest within-group food competition was greater for females in the larger group. Frequency of inter-group encounters was lower for the larger group than for the smaller group, suggesting that the larger group faced a lower level of between-group food competition.

6.2 Methods.

a) Study subjects and data collection.

The sub-adult/adult females living in Nina A (hereafter, smaller group: N = 8) and Kw (larger group: N = 20) groups were the subjects of this study (see Chapter 2 for details of the study animals). Given that seasonal variations in food abundance and distribution may affect social behaviour, data on the two groups were gathered during the same period of time. Data were collected from January 24th to May 4th 2002 on the social interactions among the group females (i.e. grooming interactions, grooming solicitation, groomer/groomee displacements and aggressive behaviour; see Chapter 2 for definitions), using focal animal sampling (Altmann, 1974; Martin and Bateson, 1993). A grooming solicitation was considered to be successful when less than 10 sec passed between the solicitation and the beginning of the grooming episode.

b) Data analysis.

At the end of the study period a total of 69.06 hrs of focal observations was collected on females in the smaller group (8.63 ± 0.15 mean hrs of observation per female ± SE; see Table 2.1) and 139.76 hrs on females in the larger group (6.99 ± 0.17 hrs per female).

For each female the number of grooming partners towards which grooming was directed was calculated (regardless of how long the grooming episodes lasted) along with the average grooming bout length. The Shannon-Wiener diversity index was used to analyse grooming equality in the two groups (see Chapter 5 for a description of the index). In total, 865 episodes of grooming solicitations were observed in the larger group and 405 episodes in the smaller group. The proportion of successful grooming solicitation (see above for definition) was obtained by dividing the number of successful solicitations by the total number of solicitations performed by each female.

A series of row-wise matrix correlations was used to analyse the relationship between grooming and social status, and the occurrence of grooming reciprocation (see Chapter 4). In order to test whether grooming reciprocation, and the relationship between grooming and social status were stronger in one of the two groups I compared the individual tau-values (obtained from the row-wise matrix correlations) between the two groups using a Mann-Whitney test. The individual tau-values measure the contribution of each female to the relationship between two variables. This analysis may thus give useful indications on whether grooming distribution differed between the two groups.

6.3 Results.

Females in the larger group spent a significantly greater amount of time grooming than females in the smaller group (Mann Whitney test: $U = 0.01$, $N_1 = 8$, $N_2 = 20$, $p < 0.001$; Figure 6.1). The number of grooming partners was non-significantly larger for females in the larger group than for those in the smaller group ($U = 45.0$, $N_1 = 8$, $N_2 = 20$, $p = 0.069$; Figure 6.2). However, on average females in the smaller group groomed 65.6% of group-females whereas females in the larger group only groomed 32.8% of potential female partners. In light of this evidence, the number of grooming partners was divided by the total number of potential partners in each group (i.e. $N = 7$ for the smaller group and $N = 19$ for the larger group) in order to obtain the relative number of grooming partners per

female. Following this correction, the relative number of grooming partners was greater for females in the smaller group than for those in the larger group ($U = 2.0$, $N_1 = 8$, $N_2 = 20$, $p < 0.001$; Figure 6.3). Grooming distribution was significantly different between the two groups when using the Shannon-Wiener diversity index: grooming equality was much greater for females in the smaller group than for those in the larger group ($U = 38.0$, $N_1 = 8$, $N_2 = 20$, $p < 0.05$; Figure 6.4). Despite the different distribution of grooming among the potential female partners, the average grooming bout length was not significantly different between the two groups ($U = 64.0$, $N_1 = 8$, $N_2 = 20$, NS; Figure 6.5).

Figure 6.1: Percentage of time spent grooming for females in the smaller (N = 8) and in the larger group (N = 20; mean percentage of scan samples ± SE).

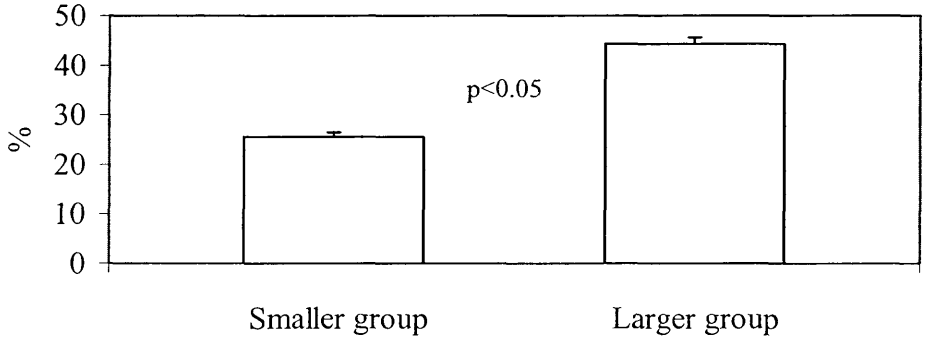


Figure 6.2: Number of grooming partners for females in the smaller (N = 8) and the larger group (N = 20; mean number of female partners ± SE).

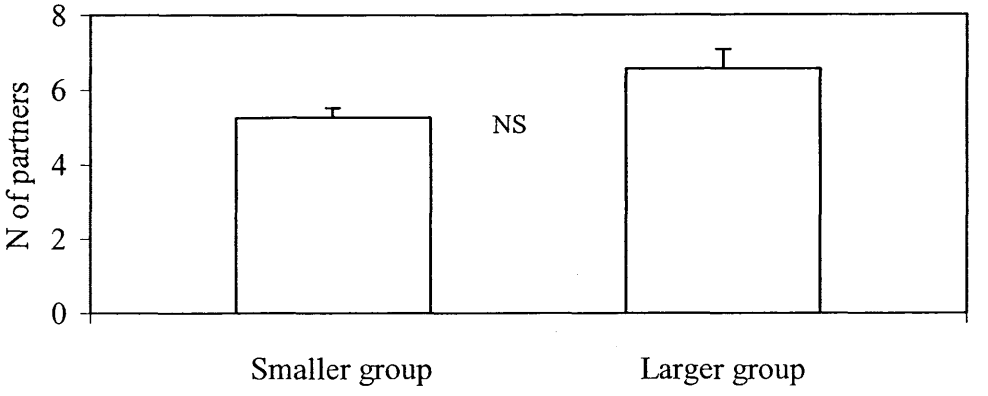


Figure 6.3: Relative number of grooming partners (see text for details) for females in the smaller (N = 8) and in the larger group (N = 20; mean proportion ± SE).

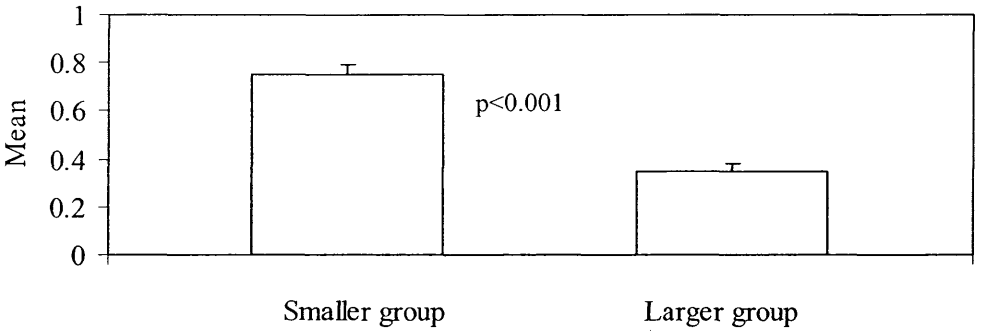


Figure 6.4: Shannon-Wiener diversity index for females in the smaller (N = 8) and the larger group (N = 20; mean grooming diversity ratio ± SE).

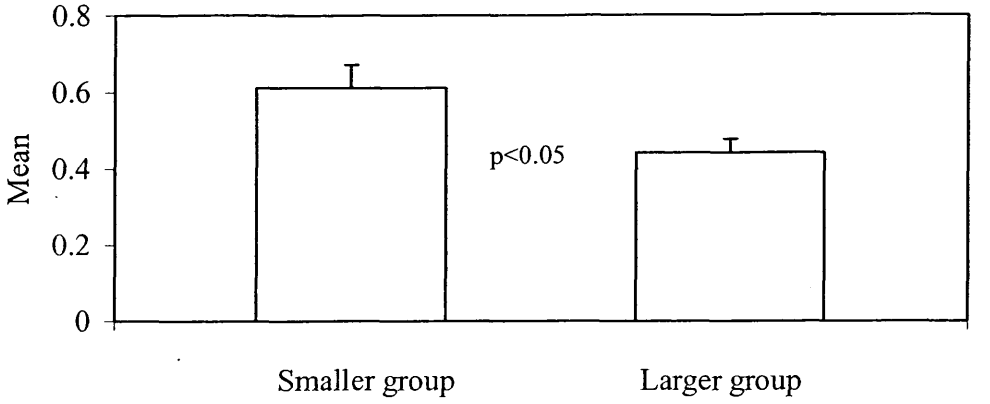
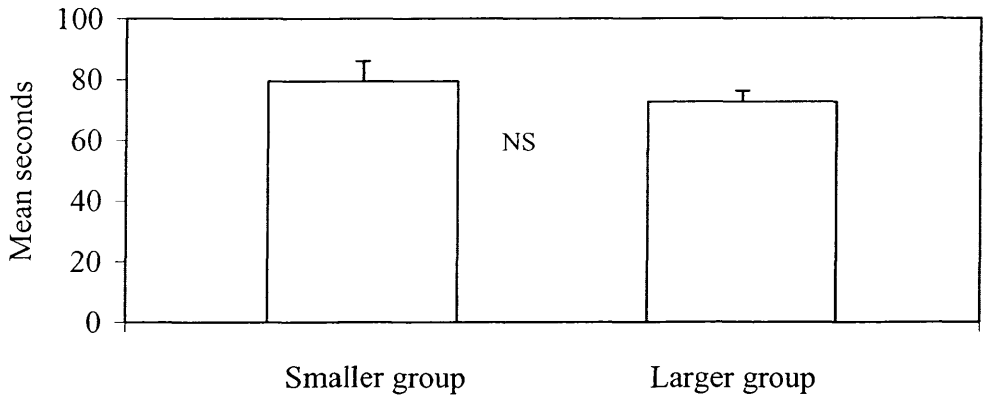


Figure 6.5: Grooming bout length for females in the smaller (N = 8) and in the larger group (N = 20; mean seconds ± SE).



In order to investigate the relationship between grooming and social status a series of analyses was run. First, a significant correlation was found between the amount of grooming given by each female and the rank of the groomees in the two groups (row-wise matrix correlation for the larger group: $Tau_{rw} = -0.10$, $p <$

0.05; for the smaller group: Tau_{rw} = - 0.24, $p < 0.05$; Table 4.1a, b, Appendix B.9 and B.10). The individual tau-values obtained from the correlation between grooming given and rank of the groomee did not differ between the two groups (U = 53.0, $N_1 = 8$, $N_2 = 20$, $p = 0.169$; Figure 6.6). Therefore, in both social groups females tended to direct grooming up the hierarchy. A row-wise matrix correlation, between rank of the groomees and the difference between grooming given and received by each female, approached significance for females in the larger group (Tau_{rw} = - 0.09, $p = 0.067$; Appendix B.3b and B.10). On the other hand, rank of the groomees was not related to the difference between grooming given and received for females in the smaller group (Tau_{rw} = - 0.19, NS; Appendix B.3a and Table 4.1b). However, the individual tau-values did not significantly differ between the two groups (U = 56.0, $N_1 = 8$, $N_2 = 20$, NS; Figure 6.7). The two groups gave similar and significant results when the relationship between grooming given by each female and the unsigned rank distance between the groomer and the groomee was analysed (larger group: Tau_{rw} = - 0.19, $p < 0.01$; smaller group: Tau_{rw} = - 0.35, $p < 0.05$). No difference was found between the two groups when the tau-values were compared (U = 54.0, $N_1 = 8$, $N_2 = 20$, NS; Figure 6.8).

Figure 6.6: Tau-values of the relationship between grooming given and rank for females in the smaller (N = 8) and in the larger group (N = 20; mean tau-values ± SE).

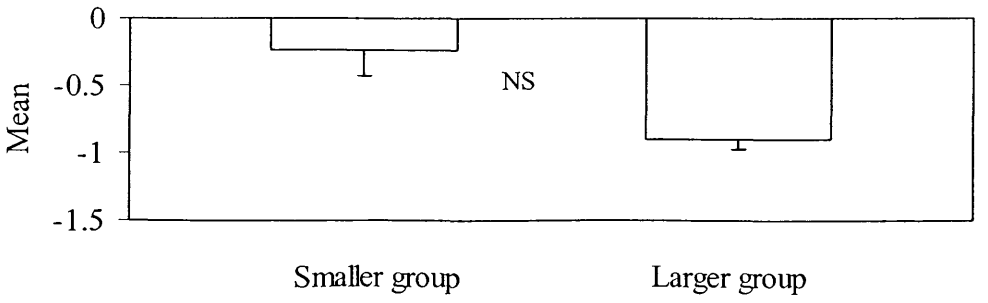


Figure 6.7: Tau-values of the relationship between the difference between grooming given and received and rank for females in the smaller (N = 8) and in the larger group (N = 20; mean tau-values ± SE).

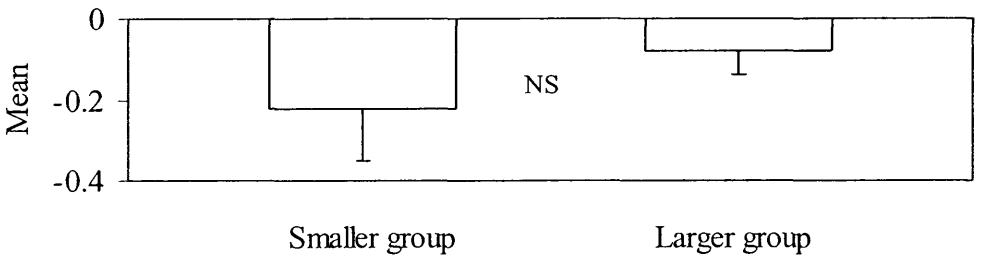
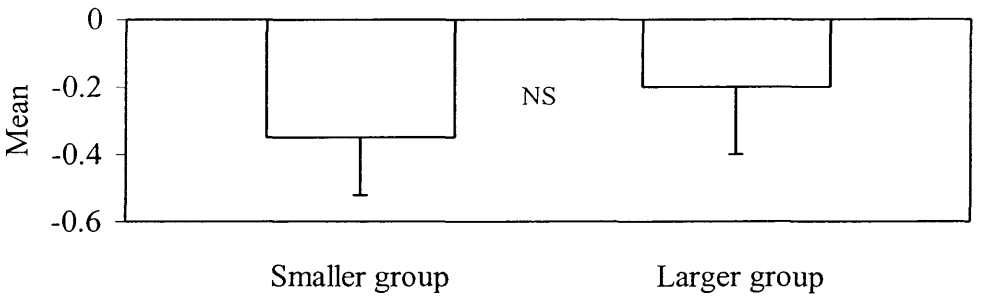


Figure 6.8: Tau-values of the relationship between grooming given and unsigned rank distance for females in the smaller (N = 8) and in the larger group (N = 20; mean tau-values ± SE).



Grooming solicitation was used to investigate females' "choice" for particular grooming partners. The frequency of grooming solicitation was almost significantly related to the rank of the female receiving the solicitation in the larger group (Tau_{rw} = -0.09, p = 0.050; Appendix B.10 and B.11b) but not in the

smaller group (Tau_{rw} = -0.06, NS; Table 4.1b and Appendix B.11a). The two groups did not significantly differ in terms of individual tau-values (U = 76.5, N_1 = 8, N_2 = 20, NS; Figure 6.9). A negative relationship was found between frequency of grooming solicitation and the unsigned rank distance between the female giving and the female receiving the solicitation in the larger group (Tau_{rw} = -0.22, $p < 0.001$). A similar significant result was found in the smaller group (Tau_{rw} = -0.40, $p < 0.01$). This relationship was almost significantly stronger in the larger than in the smaller group as suggested by the analysis of the individual tau-values (U = 45.0, N_1 = 8, N_2 = 20, p = 0.075; Figure 6.10). A significant negative relationship was found between proportion of successful grooming solicitations and rank of the female receiving the solicitation in the larger group (Tau_{rw} = -0.13, $p < 0.05$; Appendix B.10 and B.12b). No such relationship was found for females in the smaller group (Tau_{rw} = -0.14, NS; Table 4.1b and Appendix B.12a). Again, the individual tau-values did not differ between the two groups (U = 73.5, N_1 = 8, N_2 = 20, NS; Figure 6.11). Finally, proportion of successful grooming solicitation was greater the smaller the unsigned rank distance between the two females in the larger group (Tau_{rw} = -0.18, $p < 0.01$). The same analysis gave an almost significant relationship for the smaller group (Tau_{rw} = -0.24, p = 0.060). Again, no difference was found between the two groups (U = 66.0, N_1 = 8, N_2 = 20, NS; Figure 6.12).

Figure 6.9: Tau-values of the relationship between frequency of grooming solicitation and rank for females in the smaller (N = 8) and in the larger group (N = 20; mean tau-values ± SE).

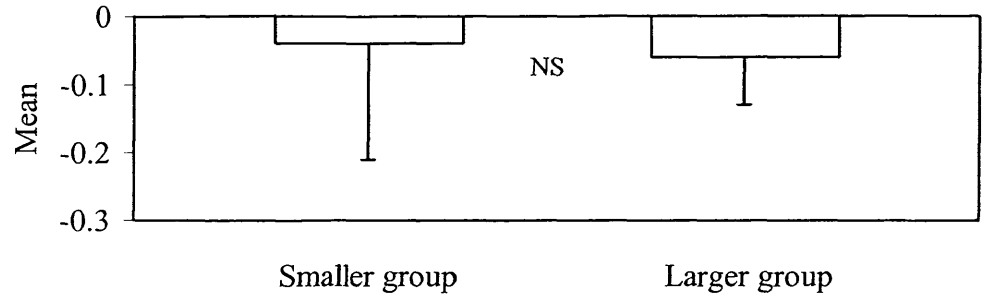


Figure 6.10: Tau-values of the relationship between frequency of grooming solicitation and unsigned rank distance for females in the smaller (N = 8) and in the larger group (N = 20; mean tau-values ± SE).

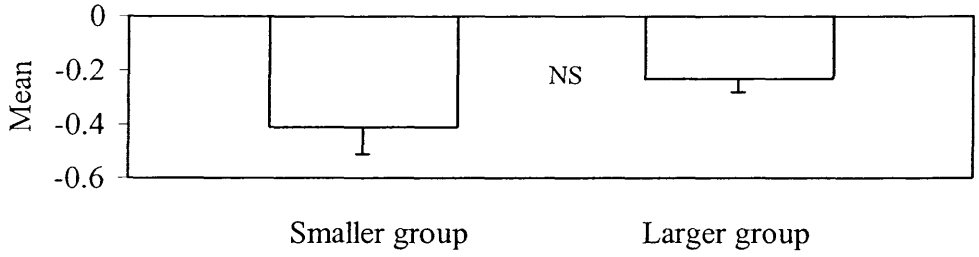


Figure 6.11: Tau-values of the relationship between proportion of successful grooming solicitations and rank for females in the smaller (N = 8) and in the larger group (N = 20; mean tau-values ± SE).

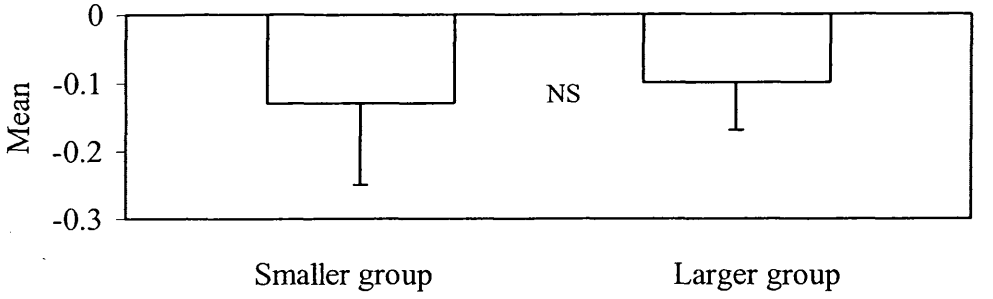
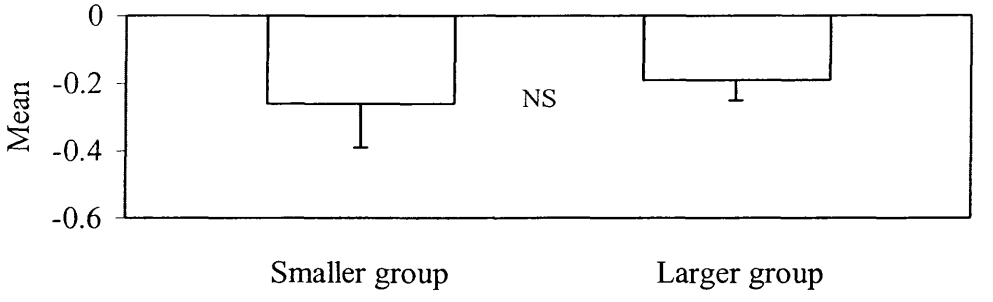


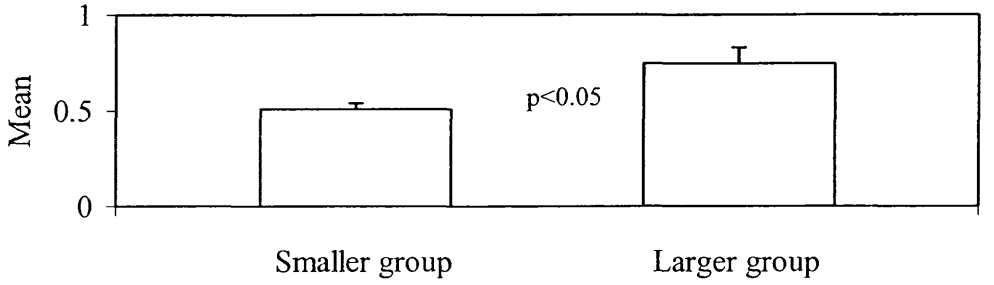
Figure 6.12: Tau-values of the relationship between proportion of successful grooming solicitations and rank for females in the smaller (N = 8) and in the larger group (N = 20; mean tau-values ± SE).



Grooming reciprocation was analysed in the two groups, with similar results: there was a significant time matching between grooming given and received in both the larger (Tau_{rw} = 0.75, $p < 0.001$; Appendix B.9) and the smaller group (Tau_{rw} = 0.51, $p < 0.001$; Table 4.1a). Tau-values were significantly greater in the

larger group than in the smaller group ($U = 28.0$, $N_1 = 8$, $N_2 = 20$, $p < 0.05$; Figure 6.13). This analysis suggested that grooming was more reciprocated among females in the larger group than in the smaller one.

Figure 6.13: Tau-values of the relationship betweeen grooming given and received for females in the smaller (N = 8) and in the larger group (N = 20; mean tau-values ± SE).



In order to analyse if and how the level of competition differed in the two groups, two analyses were run. First, frequency of aggression given or received by the females, regardless of the context in which they happened (e.g. during grooming time or foraging time), was used to analyse the overall rate of aggression among group females. Frequency of aggression was greater in the larger than in the smaller group, but this difference was not significant ($U = 322.5$, $N_1 = 8$, $N_2 = 20$, $p = 0.095$; Figure 6.14). Second, the frequency of groomer/groomee displacement (see Chapter 2 for definition) was compared between the two groups, as this behaviour is considered to be a reliable measure of the level of competition for grooming partners in social primates (e.g. Henzi *et al.*, 2003). It emerged that the frequency of displacements was approximately equal for the larger and the smaller group ($U = 76.5$, $N_1 = 8$, $N_2 = 20$, NS; Figure 6.15).

Figure 6.14: Frequency of aggression given or received for Nina A (N = 8) and Kawahara (N = 20) females (mean events / hr ± SE).

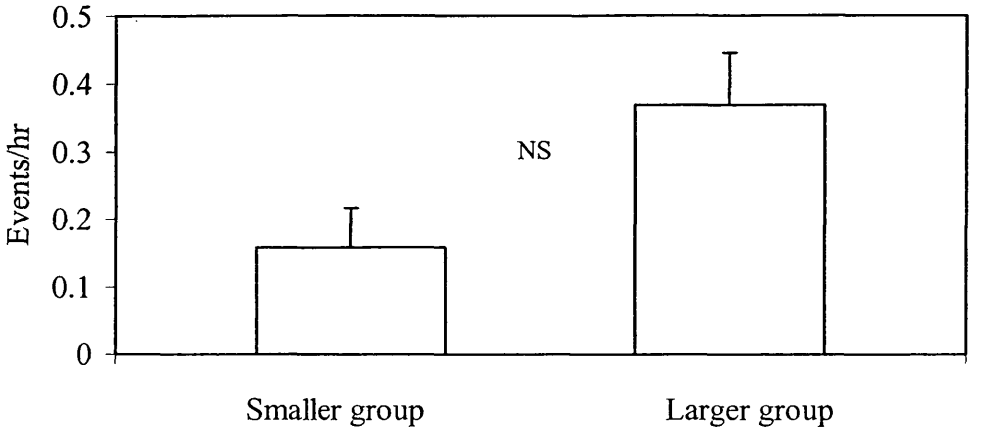
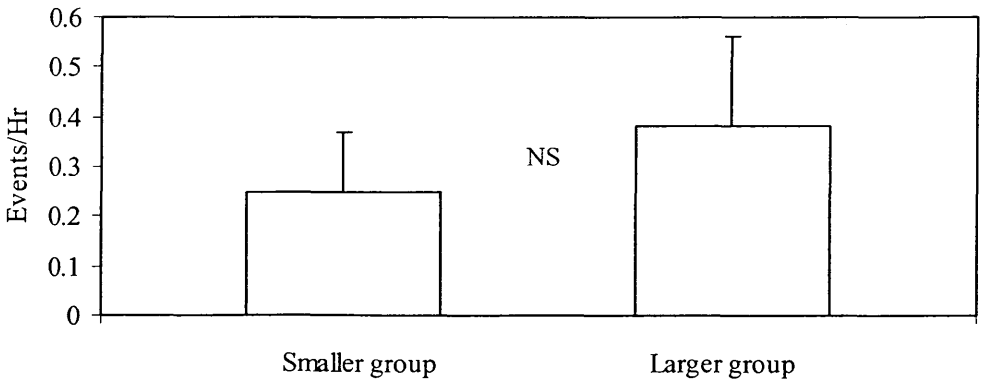


Figure 6.15: Frequency of groomer/groomee displacement for females in the smaller (N = 8) and in the larger group (N = 20; mean frequency ± SE).



6.4 Discussion.

This study represents, to my knowledge, one of the few analyses of the effect of group size on various aspects of grooming distribution. Indeed, most of the previous studies on this topic concentrated their attention simply on how group size affects time spent grooming and grooming equality (Henzi *et al.*, 1997). Data presented here indicate that group size only partially affects grooming allocation among female Japanese macaques. As predicted by theoretical models (e.g. Dunbar, 1988), females in the larger group devoted more time to grooming than females in the smaller group. The comparable frequency of groomer/groomee displacement in the two groups indicated that the level of competition for grooming partners was similar. Moreover, the overall frequency of aggression did not significantly differ between the two groups. These results indicate that the greater amount of time spent grooming by females in the larger group in comparison to those in the smaller group was probably a consequence of the increased number of potential partners rather than due to a different level of competition between the two groups (which could result in a different amount of grooming exchange given the important role of grooming as a mechanism of appeasement and of tension reduction; e.g. Dunbar, 1991; Terry, 1970). Grooming equality and relative number of grooming partners were both lower among females in the larger group than among those in the smaller group. As such, females concentrated their grooming to some preferred partners rather than trying to maintain amicable social relationships with all or many group mates, as shown by the fact that the Shannon-Wiener diversity index was relatively far from 1 (a value indicating a completely equal distribution of grooming among the group females). In order to analyse the possible benefits and costs of concentrating grooming to some preferential partners, we should know the minimum amount of grooming that two monkeys have to exchange in order to perceive their relationship as "friendly" (Chapais *et al.*, 1995). Indeed, to my knowledge, no study has ever attempted to experimentally analyse how the quality of social relationships deteriorates or improves according to the amount of grooming exchanged (although a similar attempt has been made with reconciliation; Cords

and Thurnheer, 1993), despite the large literature available on grooming in social primates. For example, if well-balanced affiliative activities resulted in such a small amount of grooming given to all the potential partners that none of them may be considered as a "friend", then this attempt to groom equally would not be particularly beneficial. In such a situation, females should groom some group members while ignoring others. Another factor playing against grooming equality may be that the absence of amicable relationships with some group members gives no costs to females. This may happen when the lack of a grooming relationship between two females simply results in their mutual avoidance but not in any kind of competition between them. In this case, the best strategy for a female would again be to concentrate her grooming effort towards some preferential partners (e.g. close kin; e.g. Call *et al.*, 1996; Defler, 1978; Dunbar, 1991) while ignoring all the other females. In this view, it is possible that the two study groups largely differed in the size and/or the number of matrilines. This factor could potentially be the main reason why grooming equality was significantly discrepant between the two groups (Silk *et al.*, 1999). Unfortunately, to date no data are available on the genetic relatedness of females in the larger group and thus this factor cannot be ruled out. Another potential source of bias in my results might be related to the operational sex ratio (OSR; see Table 1.1 for a definition and Chapter 2) of the two study groups. Hemelrijik and Luteijn (1998) showed that grooming distribution among females may be affected by the number of adult males in a group. Males, particularly in species where they are significantly larger than females, may represent more valuable alliance partners. Thus, females may concentrate their grooming towards some males at the expenses of grooming other females. This effect is expected to be stronger the larger is the ratio between the number of adult males / females in a group. This factor, however, is unlikely to be important in this study on the basis of two considerations. First, OSR only slightly differed between the two study groups (Chapter 2). Second, OSR has been observed to be not a particularly important factor affecting grooming distribution among female Japanese macaques (Takahashi and Furuichi, 1998), probably as a consequence of the small difference in body size between the two sexes (see Section 1.5b).

In any case, the findings of this study are in line with what has been found by Henzi and colleagues (1997) in five baboon groups of different size (although data presented here were collected on two groups only). They found that grooming equality and the number of grooming partners increased linearly up to a point where the trend disappeared or slightly inverted (see Section 6.1). Interestingly, the inversion point corresponded to a group composed of 10-12 females and, thus, somewhere in the middle between the number of females in the two groups of this study. Henzi and colleagues argued that this decrease in grooming equality weakens the social network of a group and, eventually, forces females to fission (Henzi *et al.*, 1997a). The different grooming equality observed in the two groups of this study support the hypothesis, although not conclusively, that social factors alone can potentially set an upper limit to group size in social primates (Kudo and Dunbar, 2001; Nakamura, 2000; 2003).

Although grooming equality and time spent grooming differed between the two groups, no other significant difference was found in terms of grooming distribution. In particular, in both the study groups grooming was highly reciprocated, mainly directed up in the hierarchy and towards females ranking close to the groomer. Moreover, the analyses of the distribution of grooming solicitations and their proportion of success revealed that females "prefer" to receive grooming, and are more likely to succeed in their attempts, from females ranking higher than, or closer to themselves (although this pattern was less evident for females in the smaller group). The fact than primates tend to exchange grooming with high-ranking group members or with those of similar rank has already been observed in many studies (e.g. de Waal and Luttrell, 1986; Seyfarth, 1980; Schino, 2001; but see Parr *et al.*, 1997 for a different result in capuchin monkeys). Overall, these results indicate that grooming clique size of a female is influenced by her own group size, while partner choice (i.e. higher-/close-ranking individuals) and the pattern of grooming exchange (i.e. reciprocation) remain unaffected.

These findings raise many considerations. Grooming reciprocation seems very important for maintaining stable amicable relationships because it may be considered as a payoff currency in its own right. This is presumably due to the

direct benefits it provides through the removal of ectoparasites and in terms of ß-endorphin release (see Chapters 1, 4 and 5). This could also be the reason why grooming reciprocation is independent from variations in the level of between- or within-group competition. The same can be said for partner choice, given its consequences on individual fitness (Muroyama, 1991). As such, the way in which females distribute their grooming to the other group mates is less affected by group size than by the birth of an infant or by the mating season (D'Amato *et al.*, 1982; Mehlman and Chapais, 1988; Martel *et al.*, 1994; Muroyama, 1994). Moreover, the results of this study show interesting similarities with previous investigations conducted on baboons and other primate species (e.g. blue monkeys, *Cercopithecus mitis stuhlmanni*; Rowell *et al.*, 1991). In a series of papers, Henzi and colleagues (Henzi *et al.*, 1997; 2003) have shown that grooming distribution in female chacma baboons is affected by group size but not by seasonal variations in the level of competition. The Japanese macaque and chacma baboon populations of these studies live in habitats differing in food productivity (i.e. sub-tropical evergreen forest versus montane grassland, respectively). As a consequence of this, the amount of time that females are able to dedicate to affiliative activities is higher among Japanese macaques than among chacma baboons (i.e. 40% of total time versus 20%). Furthermore, the kind of social bonds characterising individuals belonging to the two species is completely different and the pattern of group fission is likely to be dissimilar as well. Among Japanese macaques the strongest grooming relationships occur within matrilines and kin females usually rank close together in the hierarchy (Mehlman and Chapais, 1988; Muroyama, 1996; Koyama, 1991). Such situations produce a negative correlation between the amount of grooming exchanged within dyads and the rank distance between groomers and groomees, as seen in the present and also from other studies (de Waal, 1991; de Waal and Luttrell, 1986). In addition, females rarely exchange grooming with resident males (with the exception of mother-infant pairs or during consortship; D'Amato *et al.*, 1982; Mehlman and Chapais, 1988). On the contrary, kinship is still an important factor that regulates the quality of social relationships among female baboons (Seyfarth, 1976; Sambrook *et al.*, 1995; Silk *et al.*, 1999) but, at the same time, females form

amicable relationships with some group males that may lead to preferential mating and agonistic support (Palombit *et al.*, 1997, 2001; Smuts, 1985). Finally, Japanese macaque females of the same matriline rarely split up during fission but tend to join the same newly-formed group (Maruhashi, 1982). In baboons, females tend to join the group that has not been joined by the female who ranks immediately above them (as, by doing so, they gain at least one position in the hierarchy; Ron *et al.*, 1994) or to follow the male with whom they have a friendly relationship (Smuts, 1985). Taken together, these observations indicate that grooming reciprocation and partner choice follow similar patterns even between species differing in their behavioural ecology and social organisation. Grooming reciprocation may be essential for maintaining secure and stable social relationships (Cords and Aureli, 2000).

The persistent preference for high-ranking animals as grooming partners, found in many studies, suggests that grooming may indeed give some benefits other than grooming itself. Having found that grooming is relatively unaffected by climatic changes and by seasonal variations in activity budgets and food competition (Chapter 3 and 5, respectively) but that it may be affected by group size (this Chapter), I now aim to analyse some possible benefits of grooming exchange. This will be the topic of Chapter 7.

CHAPTER 7

WHAT ARE THE BENEFITS OF GROOMING EXCHANGE FOR FEMALE JAPANESE MACAQUES?

This Thesis' overall aim is to analyse grooming distribution and reciprocation in wild female Japanese macaques. In the previous Chapters I have analysed the potential effects of several variables on grooming exchange, namely time of day, ambient temperature, humidity, seasonal changes in resource availability, and group size. These factors have been shown to have strong, mild or no effects on grooming distribution. Whatever their effect is, however, it is evident that grooming is important for female Japanese macaques and for other species, as it is observed in all social primates (see Chapter 1). Given the complexity of social interactions between group companions it is possible that grooming is not only exchanged for itself but also for other commodities. In this Chapter, therefore, I investigate whether female Japanese macaques inter-change grooming for other benefits.

7.1 Introduction.

Social grooming as well as self-directed grooming is generally believed to have an important hygienic function (see Chapter 1). Thus, the first evolutionary selective pressure of this behaviour presumably should have been the benefits derived from the removal of ectoparasites, necrotic tissue, and receptacles of infection (Dunbar, 1996; Hutchins and Barash, 1976; Cooper and Bernstein, 2000; Henzi and Barrett, 1999). This is also supported by the fact that social grooming is often directed to those parts of the body that the receiving animal cannot easily reach by itself (Barton, 1985).

Some authors consider grooming as an altruistic behaviour (see Chapter 1) as it involves some costs to the donor (Dunbar, 1996; Matheson and Bernstein, 2000). For

example, an animal giving grooming may reduce the time it can devote to other activities (Hutchins and Barash, 1976; Noe and Hammerstein, 1994). Moreover, lactating females engaged in this social activity may reduce their level of attention towards potential risks, such as an attack by a predator or another group member on them or their offspring (Cords, 1997; Maestripieri, 1993).

On the other hand, grooming also gives some benefits to the donor, not only to the receiver, as it helps to create an atmosphere of trust and commitment between the two animals (Dunbar and Sharman, 1984; Dunbar, 1988). Indeed, social relationships among group members in some species of guenons and mangabeys (see Figure 1.1) are less tight than those observed, for example, in baboons and macaques (Oates, 1987). This is probably due to the fact that, unlike baboons and macaques, guenons and mangabeys forage for up to 80% of their daily activity and, consequently, spend less time grooming.

Regardless to the time that each species, group, or individual animal devotes to grooming, and whether or not grooming is altruistic, the fact that monkeys take risks and strive to save time for grooming in the face of compromising pressures (Sade, 1972; Dunbar and Sharman, 1984) is evidence that grooming has great biological significance for the animals involved. Indeed, discovering the functions of grooming has always been a central concern for primate socio-ecology. Seyfarth (1976; 1977) proposed, in two of seminal papers, that at least some amount of grooming provides a direct payment for other social benefits (see Chapter 1 for more details). Recent theoretical formulations, including the biological market theory, have also stressed the view that grooming may be interchanged for types of social behaviour other than grooming (see Chapter 1). The fact that monkeys groom some individuals more than others and, in particular, the relation between dominance rank and the overall direction of grooming that has been found in many studies (e.g., Boccia *et al.*, 1982; Leinfelder *et al.*, 2001; Schino, 2001; Schino *et al.*, 2003; Sparks, 1967), including this present work (see Chapters 4, 5 and 6), suggest that grooming may be a means to obtain rank-related beneficial services. Indeed, if this was not the case then grooming should not be biased towards animals ranking higher than the donor.

Studies conducted in the last three decades have mainly focused, with variable success, on determining whether grooming promotes tolerance over food and/or agonistic support. A reduced risk of aggression and harassment from other females may be considered a form of social tolerance (Barrett *et al.*, 2002; Silk, 1982) that may be actively sought by low-ranking animals. Indeed, the aggressiveness of dominant individuals during foraging can be detrimental to the reproductive success of subordinate females as it may result in a reduced foraging efficiency (see Table 1.1; Gygax *et al.*, 1997; de Waal, 1986). Consequently, monkeys may strive to trade tolerance over food sources with grooming (Barrett *et al.*, 2002; Belisle and Chapais, 2001). Following the same idea, various authors (e.g. de Waal, 1986; Koyama & Dunbar, 1996; Mayagoitia *et al.*, 1993) found that primates increased grooming time in anticipation of imminent feeding, indirectly suggesting that grooming may help to reduce the risk of conflicts over food among group members. The relationship between grooming and tolerance over food, however, is still far from being conclusively demonstrated. The difficulty of analysing the interchange of grooming for other benefits depends on the fact that the possible benefits of grooming usually constitute rare events (particularly for agonistic support, see below) and/or are not easily to record. Indeed, tolerance near food sources may be difficult to observe in species that forage in the high canopy (as is the case of Yakushima macaques; see Chapter 1). Moreover, in order for tolerance over food sources to occur three ecological conditions have to be met (Barton *et al.*, 1996; Janson and van Schaik, 1988; Koenig *et al.*, 1998; Ron *et al.*, 1994). First, high quality food sources have to be sufficiently clumped to make it impossible for all the group members to forage on them without significantly increasing the risk of aggression. Second, alternative, low quality food has to be scattered and/or far from the group ranging paths (i.e. costly to obtain) so that animals gain more benefits (i.e. in terms of stable foraging effort) by "buying" tolerance from dominant individuals than by foraging on alternative food sources. This is particularly true in animals, such as the Yakushima macaques (see Chapter 1), living in a predator-free habitat and where the risks of being severely injured during inter-group encounters are relatively low. Under such circumstances

low-ranking animals could disperse during foraging to avoid the risk of being aggressively displaced from food sources by dominant animals. Third, valuable food sources have to be of an "intermediate" size and of sufficient abundance so that dominant animals do not have too much to lose by tolerating other animals. This is a fundamental condition if one considers grooming exchange as a means to obtain other benefits. In other words, if tolerance of subordinates over food sources results in decreased foraging efficiency for dominant females, grooming is probably a commodity of insufficient value to be interchanged for such tolerance. Indeed, the biological market theory predicts that the values of the available commodities in the market have to be relatively similar for these commodities to be exchanged.

Even more controversial is the view that grooming may favour coalition formation (Hemelrjik, 1990; Hemelrjik *et al.*, 1992; Henzi and Barrett, 1999). This benefit of grooming exchange for female primates is predicted on the basis of three different observations. First, coalitions among two monkeys against a third, individually dominant animal may help them to outrank this monkey (e.g. Faibanks, 1980; Silk, 1982). Second, coalitions between females against male aggressors are expected to be particularly beneficial, and thus likely to occur, in species where fully adult males dominate females in dyadic interactions and where two or more females may outrank a male, as in Japanese macaques (Dunbar, 1984; Harcourt and de Waal, 1992; see Chapter 1). Third, infanticide has been reported to happen in many species (see Soltis *et al.*, 2000 for a case of infanticide in Yakushima macaques). Therefore, in species where females maintain high frequencies of grooming exchange, obtain rank-related benefits (e.g. preferential access to food), are at risk of infanticide, and are subordinate to fully adult males, grooming is expected to promote agonistic support. The evidence for female-female coalitions against a third female as a common occurrence among primates has recently been questioned (Henzi and Barrett, 1999), although some studies have proved that grooming exchange increases the willingness of grooming partners to support one another during conflicts with third individuals (Di Bitetti, 1997; Linn *et al.*, 1995; O'Brien, 1993; Parr *et al.*, 1997; Silk, 1982). However, female-female coalitions directed towards males have been

frequently reported (e.g. Cheney and Seyfarth, 1990a; Dunbar, 1984; Henzi and Barrett, 1999), as a means to increase the likelihood of winning a contest against a more powerful individual. Unlike tolerance, either meaning close proximity near food resources or a decreased risk of being harassed by another female, coalitions against adult males do not require that the grooming (if ever interchanged for this purpose) is mostly directed to dominant individuals (as, on average, all females are subordinate to fully adult males). In these circumstances high-ranking females should not necessarily make better allies than lower-ranking females.

With this background in mind, the aims of this Chapter were to analyse some of the possible benefits that subordinate females may gain by grooming dominant individuals. To this end, I first analysed the relation between grooming and aggression. On one hand, grooming is expected to favour the establishment of amicable social relationships that should reduce the level of aggressive interactions between grooming partners. On the other hand, however, grooming exchange requires a reduction in inter-individual distance that might elicit aggression. Moreover, dominant females have the potential to aggressively extort grooming, thus affecting the relationship between these two behaviours. Second, I focus on the possible trade of grooming for two different benefits: tolerance over food and agonistic support against male aggressors. These analyses were performed considering the amount of grooming given by each female macaque to others throughout the study period and a) the rate of attacks directed to the groomers by high ranking groomees, b) the groomees' tolerance of groomers around food sources, c) the number of instances of support provided by groomees against male aggression towards groomers.

7.2 Methods.

a) Study subjects and data collection.

Subjects of this study were all the sub-adult/adult females living in Nina A (N = 8) and Kw (N = 20) groups (see Chapter 2 for details on the study animals). Data

were collected on Nina A females during the whole study period (i.e. 22nd June 2001 to 4th May 2002) while the data collection on Kw females was restricted to the period January 24th to May 4th 2002. Grooming exchange, aggressive behaviour, time spent in close proximity (i.e. ≤1 metre), and the number of close approaches were recorded using focal animal sampling (see Chapter 2 for definitions). The hierarchical status of each female was obtained by recording *ad libitum* all the observed dyadic agonistic interactions with a clear-cut result. A food patch was defined as a discrete area within which individuals were able to collect food continuously as they moved within it (therefore, a patch could contain more than one food type; White and Wrangham, 1988; Whitten, 1988). Every time two or more females were observed foraging on the same food patch their identity was recorded. To have a more effective measure of tolerance over food sources, I used co-feeding defined as the time two monkeys spent in close proximity (i.e. ≤1 metre) while foraging.

b) Data analysis.

Data were analysed independently for the two groups. When I analysed agonistic support I divided the number of supports received by each female by the total number of aggressive acts received by that female. This correction is essential, although rarely utilised in studies on coalition formation, as it controls for the possibility that agonistic support is simply more likely to occur the higher the level of aggression that a female receives. By following this procedure, therefore, I had a more stringent measure of a female's willingness to support another female.

Matrix comparisons by means of the row-wise Kr-test (de Vries, 1993; see Chapter 4) were used to evaluate the relation between 1) grooming given and the overall frequency of aggression received (the matrix for grooming given was the "original" matrix while that for aggression was a transposed matrix), 2) grooming received and the overall frequency of aggression performed (the transposed grooming matrix and the "true" matrix of aggressions performed). Matrix comparisons by means of the row-wise Kr-test were also employed to investigate the relation between grooming received (again the transposed grooming matrix) and: 1) the number of

times groomers were seen foraging in the same food patch with groomees, 2) the amount of time grooming partners spent in close proximity while foraging (i.e. co-feeding), 3) the frequency of groomers' close approaches to foraging groomees, 4) the number of agonistic supports groomers received from their grooming partners.

Then, in order to better understand the possible benefits of grooming, I restricted the analyses outlined above to the grooming directed to higher-ranking monkeys. This was because aggression, particularly in despotic species such as the Japanese macaques (see Chapter 1), is usually directed down the hierarchy. Therefore, dominant females may grant a lower risk of aggression, increased tolerance over food sources, or agonistic support to subordinate females from whom they receive most grooming. I worked with "triangular matrices". In these matrices monkeys are ordered according to their hierarchical status, so that only the upper or lower triangle of the matrix contains data. The MatMan software (Noldus Information Technology, 1998), that I used for statistical analysis of matrices (see Chapter 2), considers empty cells in the matrix as zeros, a procedure that alters the result of matrix correlations. To avoid this I followed the method proposed by Hemelrijk (1990) for triangular matrices. That is, I inserted the same fixed value in all the cells in the half of the matrix containing no data. The choice of this value was arbitrary, but the value had to be higher than any other value contained in the other half of the matrix and representing true data. Finally, I created a matrix containing a dummy variable "data-no-data" and used it as a control matrix in a series of partial row-wise matrix correlations.

In order to control for the confounding effect of kinship, in the smaller group only (as kinship was unknown in the females in the larger group; see Chapter 2), all the analyses were re-run excluding kin females (i.e. considering the cells corresponding to kin females as missing values).

7.3 Results.

a) The relationship between grooming and aggression.

A significant positive correlation was found between the amount of grooming each female directed to all her group mates and the frequency of aggression she received from those group mates in the larger group (Kendall row-wise matrix correlation: $Tau_{rw} = 0.127$, $p < 0.006$; Appendix B.9 and B.13b). The effect of kinship could not be determined as the genetic relationship of females living in the larger group was unknown (Chapter 2). A similar result emerged in the small group ($Tau_{rw} = 0.327$, $p < 0.0004$; Table 4.1a and Appendix B.13a), even when kinship was controlled for (partial row-wise matrix correlation: $Tau_{rw,xy,z} = 0.328$, $p < 0.0004$). No correlation was found between the frequency of aggression each female performed against her group mates and the amount of grooming she received from those group mates in the large group ($Tau_{rw} = 0.069$, NS). Such a relation did not appear in the small group either ($Tau_{rw} = 0.128$, NS), and this pattern remained unaltered when kinship was controlled for ($Tau_{rw,xy,z} = 0.058$, NS). Thus, females in both the larger and the smaller group mostly groomed the more aggressive individuals. It has repeatedly been reported in scientific literature that animals spending more time grooming one another are also more often in close proximity (Furuichi, 1983; O'Keefe *et al.*, 1983; Seyfarth, 1980; Troisi *et al.*, 1989). At the same time, reduced inter-individual distance increases the risk of aggression among animals in many different contexts (Calhoun, 1962; Cords and Thurnheer, 1993; Koenig *et al.*, 1998; Lorenz, 1966; Mathy and Isbell, 2001; but see Judge and de Waal, 1993; 1997 for different results). This relation between grooming, proximity and aggression may be the real cause of the higher rate of grooming directed to the most dangerous female macaques. However, if this was the case in the study groups, the females should also have attacked particularly those individuals from whom they received more grooming. Data did not support this prediction. The rank of females seems a parameter that needs to be taken into account. Indeed, aggression is mostly

directed down the hierarchy in the Japanese macaque. Therefore, interchange of tolerance for grooming can only occur with low rankers. For this reason the correlation between the amount of grooming given to group mates and the frequency of aggression received from them was analysed, using the procedure suggested by Hemelrijk (1990; see Section 7.2b). There was no relationship between the amount of grooming given to higher-ranking animals and the frequency of aggression received from them for females in the larger group (partial Kendall row-wise matrix correlation: $Tau_{rw,xy,z} = 0.050$, NS). However, a positive relationship was found between the grooming given and aggression received in the smaller group ($Tau_{rw,xy,z} = 0.450$, $p < 0.01$). This result was confirmed when kin were excluded from the analysis ($Tau_{rw,xy,z} = 0.387$, $p < 0.05$). In other words, females in the smaller group received more aggression from higher-ranking individuals whom they groomed most than from individuals whom they groomed less or did not groom at all.

In the larger group a positive relationship was found between the amount of grooming received by higher-ranking females and the frequency of their aggressive acts towards lower-ranking individuals ($Tau_{rw,xy,z} = 0.178$, $p < 0.048$). For females in the smaller group no significant relationship was found between grooming received and aggression given ($Tau_{rw,xy,z} = -0.055$, NS). When kin were excluded the result remained non-significant ($Tau_{rw,xy,z} = -0.116$, NS).

b) The relationship between grooming and tolerance near food sources.

In the larger group, a significant and positive correlation was found between the amount of grooming each female received and number of times she was seen foraging in the same food patch with her grooming partners (row-wise matrix correlation $Tau_{rw} = 0.269$, $p < 0.0001$; Appendix B.14b). Females in the smaller group were not more likely to be seen foraging in the same food patch with their preferred grooming partners ($Tau_{rw} = 0.158$, NS; Appendix B.14a). This result was unaffected when the

effect of kinship was partialled out (partial row-wise matrix correlation $Tau_{rw,xy,z}$ = 0,145, NS).

If grooming given may be used to obtain tolerance at food sources from high-ranking animals, it may be particularly beneficial for females to groom partners ranking higher than themselves as these may have the potential to effectively monopolise food sources and/or be aggressive (Chapters 4 and 5). Indeed, in species forming linear hierarchies and despotic societies, such as the Japanese macaques (Chapter 1), dominant females do not need to groom subordinate individuals, as they cannot be displaced by them from food sources. Conversely, subordinate females may increase their energetic intake and reduce the risk of aggression by grooming high-ranking individuals, if grooming is a currency that may be exchanged for other goods. In this view, the critical test of the relationship between tolerance over food sources and grooming received requires evidence of such interchange between dominant and subordinate females. To test this, a row-wise matrix correlation was run between the amount of grooming that each female received from partners ranking lower than herself and the number of times this female was observed on the same food patch with her lower ranking groomers, using the procedure suggested by Hemelrijk (1990; see Section 7.2b).

A positive and significant relationship was found between presence on the same food patch with lower ranking group mates and grooming received for females in the larger group ($Tau_{rw,xy,z} = 0.396$, $p < 0.0001$). A similar relationship was found for females in the smaller group ($Tau_{rw,xy,z} = 0.400$, $p < 0.042$). Again, this significant result was confirmed when kin females were excluded from the analysis ($Tau_{rw,xy,z} = 0.403$, $p < 0.023$).

All the previous analyses did not take into account inter-individual distances between females during foraging. Following its definition (Section 7.2), a food patch may potentially include many trees and a large proportion of the canopy. Therefore, two females may forage on the same patch even though no tolerance regarding food sources is required. That is, a food patch might be so large that monkeys simply

cannot see each other in it, so that the chances of contest food competition are reduced. In order to further explore the above findings, therefore, the relationship between grooming received and the amount of time two females spent in close proximity (i.e. ≤ 1 metre; see Chapter 2 for definitions) while foraging, or the frequency of close approaches during foraging, respectively, was analysed in a series of statistical tests.

Percentage of time spent in close proximity when the groomees were foraging was very low (means + SE of hours spent in close proximity with foraging groomees divided for the hours of observation on groomees: 0.022 + 0.005 for the small group and 0.001 + 0.000 for the large group), and close approaches were rare events (means + SE of the number of close approaches per hour of observation: 0.006 + 0.001 for the small group and 0.001 + 0.000 for the large group). However, no aggressive interactions were observed when two or more females were foraging in close proximity or following close approaches by subordinate monkeys. A row-wise matrix correlation between the amount of time the groomers spent in close proximity with the groomees, when the groomees were foraging, and the amount of grooming received by each female, was run. The two variables were positively correlated in the large group ($Tau_{rw} = 0.384$, $p < 0.0001$; Appendix B.15b) but not in the small one ($Tau_{rw} = 0.171$, NS; Appendix B.15a) even when kinship was controlled for ($Tau_{rw} = 0.107$, NS). Again, in order to investigate grooming and tolerance interchange between lower and higher ranking individuals, I measured the correlation between the amount of grooming that each female received from her subordinate partners and the number of times that that female was observed in close proximity with lower-ranking groomers during foraging. These two variables were highly related for females of the larger group ($Tau_{rw} = 0.423$, $p < 0.0001$), suggesting that grooming given does increase tolerance in close proximity during foraging. The same significant result was found for females in the smaller group ($Tau_{rw} = 0.378$, $p < 0.023$), even when kinship was controlled for ($Tau_{rw,xy,z} = 0.419$, $p < 0.007$).

In addition to these findings, I found a significant correlation between the quantity of grooming received by each female and the number of groomers' close approaches to the groomees, when the groomees were foraging, for females in the larger group ($Tau_{rw} = 0.306$, $p < 0.0001$; Appendix B.16b). Moreover, the correlation was also highly significant for females in the smaller group ($Tau_{rw} = 0.237$, $p < 0.034$; Appendix B.16a). However, this result was not significant when controlling for kinship ($Tau_{rw,xy,z} = 0.121$, NS). Finally, in order to re-evaluate this kind of interchange between dominant and subordinate group-mates, I correlated the amount of grooming that each female received from females ranking lower than her and the number of close approaches she received by those subordinated groomers. There was a significant positive relationship in both the larger ($Tau_{rw,xy,z} = 0.361$, $p < 0.0007$) and the smaller group ($Tau_{rw,xy,z} = 0.518$, $p < 0.008$). The result was not affected by the exclusion of kin females ($Tau_{rw,xy,z} = 0.490$, $p < 0.007$). Therefore, during foraging subordinate females approached mostly dominant females whom they groomed most.

c) The relationship between grooming and support against male aggressors.

For the females in the larger group I observed 81 agonistic interactions in the period from January to May 2002 (Chapter 2). In 23 of these interactions (i.e. 28.3 %) a third female supported a female victim against an aggressor. The aggressor was a male in 18 (17 adult males plus 1 sub-adult male) of these aggressive interactions followed by a support (i.e. 78.2 %). Only agonistic supports received when a male was the aggressor were considered in the following analyses to compare the results between females in the smaller and in the larger group (given that no agonistic support against female aggressors was observed in the smaller group; see below). The number of agonistic supports received by each female was divided by the total number of male aggressions received by that female. After this correction, a correlation was run between grooming received by each female and the number of agonistic supports she performed in favour of her grooming partners, against male

aggressors. A significant and positive relationship was found between those variables in the larger group ($Tau_{rw} = 0.288$, $p < 0.0001$; Appendix B.17b), showing that female Japanese macaques received more agonistic support from those female companions to whom they directed most grooming.

In the smaller group I observed 312 agonistic interactions involving females during the study period (i.e. from June 2001 to May 2002; Chapter 2). In 26 of these interactions (i.e. 8.3 %) a third female supported the victim against an aggressor (see Chapter 2 for a definition of agonistic support). In 100 % of these aggressive interactions the aggressor was a male: 2 aggressions were by a sub-adult male and the remaining 24 were by an adult male. A positive and significant correlation was found between grooming received and agonistic support given ($Tau_{rw} = 0.254$, $p < 0.036$; Appendix B.17a). Agonistic support is thought to be more likely to occur among closely related individuals than among distantly related or unrelated individuals, given the beneficial consequences that support and coalitions have on the inclusive fitness of an individual. This issue could not be analysed for females in the larger group (Chapter 2). However, when the effect of kinship was controlled for in the smaller group, the relationship between grooming given and support received became non significant ($Tau_{rw,xy,z} = 0.070$, NS).

7.4 Discussion.

In this Chapter I analysed the possible benefits of grooming exchange for female macaques. Although of variable strength and with a variable effect of kinship on the results, grooming was positively related to aggression, to tolerance around food and to agonistic support. A possible explanation for the relationships found is that grooming is a means to establish social bonds with some other group members that give some benefits (e.g. tolerance or agonistic support) to the animals forming such

bonds. The fact that grooming was also positively related to aggression, however, may contradict this picture (see below).

The formation and benefits of social bonds between group members may be viewed from two perspectives, which basically differ form one another in the importance they give to the short-term and long-term consequences of social relationships. One view considers social relationships as a consequence of an active choice and selection, made by each animal, of the "best" possible partners (in terms of benefits that these partners may give to that animal). According to this view, animals invest in social relationships according to the benefits they "plan" to gain from them. It follows that an individual's choice of the group mate to whom it directs grooming might be based on the generalised memory of its past experiences with others animals and on the ability to use these past experiences in order to avoid cheating (de Waal and Luttrell, 1988). This view is supported by many observations and experiments indicating that monkeys are indeed able to remember past events and to solve a wide variety of problems (Tomasello and Call, 1997). Moreover, monkeys seem to have at least some understanding of the existing bonds between other individuals (Bergman *et al.*, 2003; Cheney and Seyfarth, 1990b; Dasser, 1988). If this is true and other conditions being equal (e.g. differences in "resource holding potential" between individuals, see Chapter 5), the investment in a relationship by each animal within a given dyad may be highly asymmetrical on a short-term basis but should be relatively symmetrical in the long run. For example, one animal may groom another and not receive anything in exchange (e.g. either grooming or other benefits) when the grooming session is finished, while having some benefit later in the future. A second view suggests that the process of building up good relationships does not necessarily require complex cognitive skills, good memory or the ability to plan strategically for the future (Barrett and Henzi, 2002). Social bonds and the exchange of various benefits may simply reflect the operation of an evolutionary "rule of thumb", namely, "when a female establishes a bond with a higher-ranking partner, it states something along the lines of 'groom the dominant group-mates', a rule maintained by natural selection and of which the female herself is not aware"

(Barrett and Henzi, 2002; p. 275). The result would be the formation of a fitness-enhancing grooming bond, as having good relations with dominant females may be highly beneficial. If monkeys do not remember past interactions, cheating may only be avoided by exchanging benefits on an immediate or short-term basis. Put in a simple example, a monkey grooms another, dominant, monkey and immediately afterwards the two animals both forage on the same food source without any competition.

Besides some attempts to consider these two views as alternatives (Barrett and Henzi, 2002), distinguishing between the short- and long-term benefits of social relationships may be difficult, if not impossible (see Chapter 5). Social primates may interact repeatedly during the course of the day and over several consecutive days, making it impossible to distinguish between the short- and long-term effects of such interactions. Indeed, we have no evidence upon which to base any timeframe for reciprocity in primates: should it be minutes, hours or days? For example, if a female grooms another monkey but this grooming bout is not seen to be exchanged for grooming or for other commodities, it is difficult, if not impossible in the wild, to tell whether this lack of exchange is due to differential investment in the relationship or to lack of opportunity to exchange grooming for other benefits (e.g. tolerance at food sources). Moreover, how can we reliably estimate the time window necessary to distinguish a short- from a long-term benefit? In theory, in the case of grooming interchanged for other commodities, we could record the type of social interactions between two animals in the period immediately after one monkey has groomed the other (and this grooming has not been reciprocated) and before a new grooming session starts between these same two animals. Even in this case, the time window may last a few seconds or many days, and an opportunity for interchange may occur or may not. The point, therefore, is that any distinction between short-term and long-term benefits and planning is arbitrary and a topic that can be difficult to address. To my knowledge, no study has effectively solved this problem conclusively. If at all possible, such a study can only be conducted in a captive setting where interactions

among animals may be controlled through, for example, temporary and selective separations of some animals.

a) The relationship between grooming and aggression.

The relationship between grooming, proximity and aggression has been the topic of intense research and of great debate. Classical ethological views considered aggression to increase when inter-individual distances decreased (Lorenz, 1966). More recently, some studies conducted on primates under crowding conditions have demonstrated that this may not be true. For example, in rhesus macaques aggression does not increase when crowding is artificially increased by reducing enclosure size whereas rates of grooming do so (Judge and de Waal, 1993; 1997). Grooming also increases in the minutes before feeding in captive chimpanzees, *Pan troglodytes* (Koyama and Dunbar, 1996), and especially when food is clumped, suggesting that this species is able to foresee and limit the potential risk, on group stability, of conflicts caused by food competition. Unfortunately, no similar study has been conducted on the Japanese macaque. Finally, grooming performed as a means of post-conflict reconciliation decreases the chances of renewed aggression (e.g. Aureli and van Schaik, 1991; Kutsukake and Castles, 2001). Grooming, therefore, may serve to keep aggression under control when the risk of conflicts is likely to increase. This is particularly true in despotic species such as Japanese macaques (see Chapter 1), where power differential among group members is clear and aggressive interactions frequent (Henzi and Barrett, 2000).

However, the results of this study seem to contradict this picture. Lower-ranking females were more often attacked by their higher-ranking grooming partners in both study groups. Such a relationship between grooming given and aggression received has, however, been found in other studies (Perry, 1996; Silk, 1982), including one on a captive group of Japanese macaques (Schino *et al.*, 2005). My finding raises the possibility that dominant individuals may extort grooming from subordinates by force (given the intrinsic value of this behaviour; see Chapter 1), as a positive relationship was found between frequency of aggression and amount of grooming exchanged

between two monkeys in both the study groups. This possibility has already been proposed by Silk (1982) as an explanation of the tendency for grooming to be directed up the hierarchy. Grooming extortion may considerably reduce the chance of free trading of biological commodities, as Henzi and Barrett (2002) pointed out for chacma baboons. In this species, higher-ranking individuals were able to obtain access to other females' infants (that are often very "attractive" for them) with little or no prior grooming. Dominant coercion may actually be used to disrupt any grooming market effect, as free trading of biological currencies is determined by the dominant individuals' capability to extort beneficial behaviours from subordinates. This is an essential point to consider since dominance hierarchies are very common in primate groups and other social animals, and these group-living situations are the ones in which a biological market approach is likely to be most productive (Barrett *et al.,* 2000). Therefore, the potentially distorting impact of grooming coercion has to be taken into account by future studies if the biological market model is to be fully applicable to social animals.

b) The relationship between grooming and tolerance near food sources.

The results of this study convincingly indicated that grooming may significantly increase tolerance around food sources: presence on the same food patch, close proximity during foraging (i.e. co-feeding), and frequency of close approaches by subordinate individuals to dominant ones during foraging were positively correlated with the amount of grooming that female Japanese macaques gave to group mates ranking higher than themselves. Moreover, similar findings were obtained in two groups of different sizes, suggesting that the relationship between grooming and tolerance was not simply due to one study group but a rather general phenomenon. Finally, kinship (only known for the females belonging to the small group) did not have any notable effect on this relationship.

A positive relationship between grooming and tolerance at food sources has been demonstrated in various studies in captivity and the wild (O'Brien, 1993; Silk, 1982). For example, groomees were more willing to share food with groomers if a grooming

session preceded food provisioning in captive chimpanzees (de Waal, 1989). Moreover, grooming restored tolerance of co-feeding to pre-conflict baseline level (Cords, 1992). Tolerance around food is often greater the higher the degree of kinship (Belisle and Chapais, 2001). Interestingly, Ihobe (1989) found no significant effect of kinship on tolerance in wild Japanese macaques, supporting our findings. Ultimately, the bias of grooming and tolerance towards kin depends on the presence and size of matrilines, a factor this study could not analyse given that kinship was only known for females in the smaller group.

The habitat characteristics of the study site at least partially meet the ecological conditions necessary for tolerance around food to take place (see above and Chapter 1). The main food trees are clumped but also occur in relatively large patches along the coastal forest of Yakushima (Agetsuma, 1998). These conditions make it likely that tolerance around food sources may not be particularly costly for dominant females. Dispersion during foraging, however, is a feasible option for Yakushima macaques to avoid direct food competition. This probably explains why the presence of two or more females on the same food sources and the number of close approaches during foraging were relatively rare events. Indeed, a parallel study on the same two groups (Majolo, 2004) demonstrated that females in the larger group were more dispersed than those in the smaller group. Besides, direct food competition was greater in the larger group. We may hypothesise that females tended to disperse to avoid aggressive interactions over food. At the same time, female "friends" tended to remain in the same sub-group. This strategy has clear advantages, as the presence of friends during group movements may reduce the risk of aggression, increase tolerance near food, and increase the chances of being supported during agonistic interactions with males (see below). Moreover, this strategy is particularly beneficial for females in the larger group, because of the greater competition for food or for grooming partners (see above and Chapter 6), a consideration that may help explain why the relationship between grooming and tolerance regarding food was stronger in the larger group. In any case, the findings of this study indicate that a relationship

does exist between grooming and tolerance around food sources, regardless of how often two or more females have a chance, or are forced, to forage nearby.

c) The relationship between grooming and support against male aggressors.

This study demonstrated a positive relationship between grooming exchanged and agonistic support against male aggressors. It is important that the number of agonistic supports observed per female was divided by the total number of aggressions received by female, a correction rarely observed in studies analysing coalition formation. When the effect of kinship was controlled for in the smaller group, however, the correlation became non-significant. Without data on kinship for females in the larger group it is not possible to analyse whether this result would be confirmed. Henzi and Barrett (1999) pointed out that there is no convincing evidence for a cause-effect relationship between grooming and agonistic support in either the wild or captivity. Prior to this, several authors (e.g. Dunbar, 1988; Dunbar and Sharman, 1984) suggested that grooming might be a mechanism by which two individuals maintain an attachment that increases the likelihood of receiving aid in competitive interactions. The problem here is that coalition formation between adult female primates has been rarely observed in wild populations. Where it has been recorded there is little indication that the females involved maintained strong grooming bonds. In many cases, the subordinates provided support to more dominant animals, which were likely to win the interaction anyway (Silk, 1982; O'Brien, 1993). Another, not dissimilar view, considers grooming and alliances as a means to decrease aggression among group members (de Waal, 1992). However, data collected so far indicate that monkeys control the level of aggression not through closely bonded individuals preferentially coming to each other's aid, but by enabling subordinate animals to enhance the levels of tolerance shown to them by dominant individuals (Silk, 1982).

Whatever the relationship between grooming and agonistic support, it is interesting that all the observed coalitions among females in the smaller group, and

most in the larger group, were against male aggressors and not against other group females. Agonistic support against males is a particularly beneficial option for female Japanese macaques in light of three considerations. First, sexual dimorphism in body size and canine length is not as important in the Japanese macaques as it is in some other primate species (e.g. baboons; Cheney *et al.*, 2004). This means that the risk of supporting another female against a male may not be particularly high. Second, and in light of the previous consideration, agonistic support against males may be an effective means to avoid or reduce the risk of infanticide (it is worth noting here that an infanticidal event was reported for Yakushima macaques few years ago, and specifically in the smaller group before its fission; Soltis *et al.*, 2000). Third, agonistic support may be favoured in this sub-species as, in Yakushima, sex ratio is greater than in other populations of Japanese macaques (Nakagawa, 1998; Sprague *et al.*, 1998; see Chapter 1). As a consequence of this, the frequency of male aggression towards females may be greater in Yakushima.

CHAPTER 8

PRIMATE SOCIAL RELATIONSHIPS IN AN EVOLUTIONARY PERSPECTIVE

8.1 Some Factors Affecting Grooming Distribution among Yakushima Macaques: A Summary.

This Thesis aimed to analyse the relative importance of various factors that may affect grooming distribution among female Japanese macaques and the benefits that grooming may give to animals exchanging it. In Chapter 3, I analysed the effect of climatic factors (i.e. time of day, ambient temperature, and relative humidity) on time spent grooming, self-grooming and scratching. While self-grooming and scratching were both significantly affected by climatic factors (although to different degrees) the overall effect of these factors on social grooming was non-significant. These results were interpreted in light of the social function of grooming and thus on the need for this behaviour to become, during the course of evolution, increasingly independent from climatic factors.
Two methodological approaches (one based on dyads and the other on matrices) for the study of grooming distribution and reciprocation were used and compared in Chapter 4. I concluded that the use of matrices is preferable for studies on social behaviour for it does not over-estimate the samples as dyadic approaches do. Therefore, row-wise matrix correlations were used in the subsequent chapters whenever the data allowed this type of analytical approach. Overall, grooming was mainly exchanged for itself in both the study groups. Seasonal changes in food abundance and diet composition did influence time spent grooming but had no effects on grooming distribution and reciprocation (Chapter 5). Thus, mild, short-term changes in habitat characteristics have minor or no effects on social relationships among group members. The aim of Chapter 6 was to determine if and how group size affects grooming distribution and reciprocation. Although females in the larger group (N = 20) spent more time grooming, they concentrated

their grooming on fewer partners, relatively to group size, than females in the smaller group (N = 8). Grooming was more reciprocated among females in the larger group than among females in the smaller group. The results of this study thus demonstrate the importance of group size as a factor affecting social relationships among group members. Moreover, they show that both climatic factors and seasonal changes in habitat characteristics have mild, or no significant effect on grooming distribution. Given the importance that amicable interactions have on individual fitness (see below), this resilience may have evolved to avoid the potential disruptive effects that periods leaving insufficient time available for social interaction might have on individual relationships. With this background in mind, the aim of Chapter 7 was to analyse the possible benefits of grooming exchange for female macaques. In both the smaller and the larger group grooming exchange between two females increased the chances that they supported one another against a male aggressor. This support may give important benefits to female macaques given that the operational sex ratio (see Table 1.1 for a definition) is relatively high in Yakushima (and higher than in the populations living on the main island) and thus male attacks may be frequent (Nakagawa, 1998). In other words, adult males may represent a threat for females, particularly for lactating females, who are more at risk of infanticidal attacks, or when males aggressively attempt to coerce mating. Grooming exchange also promoted tolerance near food sources. Grooming thus gives various benefits to social partners and this explain why many primates spend a conspicuous proportion of the day exchanging it.

In conclusion, the findings of this Thesis support the view that grooming is used by primates to maintain amicable social relationships with some group members that may result in various benefits to the grooming partners. Moreover, my results emphasise the importance of the social context on the frequency and quality of social relationships, along with various non-social factors (i.e. climate or food abundance).

8.2 Primate Social Relationships: What We Know So Far and What We Do Not.

Since the beginning of the 20th century, as soon as detailed observations on primate behaviour were being collected, it became clear that primates devote a significant proportion of their time to the exchange of amicable behaviour (e.g. Zuckerman, 1932). Moreover, it was evident that grooming was the main behaviour used for these types of social interactions (Carpenter, 1942). In the second half of the last century, the rapidly growing body of data collected in the field as well as in captivity showed that different primate species present large variations in ecology, anatomy and social organisation. These differences, however, have relatively little effect on the importance of social behaviour for primates. This is true even for solitary primates (see Figure 1.1), species who were considered to spend most of their lives alone and only interact with con-specifics during mating or territory defence. Field data have shown that solitary species are capable of complex social interactions that include regular "meetings" at the sleeping holes and long-lasting contacts with neighbouring offspring (Bearder, 1987).

Robert Hinde was among the first to recognise that non-human primates, much like human beings, are capable of establishing and maintaining long-lasting amicable relationships (Hinde 1974; 1976). The type of social relationship between two animals is characterised by its value (i.e. the benefit that each animal gains from the relationship), its security (i.e. the probability that the relationship with a partner will change over time), and its compatibility (i.e. the general tenor of the relationship). Animals may maintain different relationships with different individuals depending on the various characteristics of the potential partners (i.e. genetic relatedness, sex, social status, age). Ever since the seminal works of Hinde, a large number of studies have been analysing the benefits that social relationships and grooming exchange may give to primates, including the work presented in this Thesis.

The notion that the original function of grooming was to remove the dirt from the fur and to reduce parasite loads is now generally accepted (e.g. Freeland, 1981; Hutchins and Barash, 1976). However, still open to debate is the view that

grooming is a "social tool" that primates use to obtain certain benefits. This argument has been largely discussed and examined throughout this Thesis and thus it can be briefly summarised here. Although grooming is often exchanged for itself it may also promote agonistic support (see Chapter 7; Chapais *et al.*, 1995; Hemelrijk, 1994; Silk, 1982). Moreover, grooming seems to increase tolerance at food sources, and food-sharing (see Chapter 7; Belisle and Chapais, 2001; de Waal, 1997). Animals sharing amicable relationships usually have higher frequencies of reconciled conflicts (Aureli and de Waal, 2000; Majolo 2004). Finally, mothers tend to tolerate more attempts to interact with their infants made by animals who have previously groomed them (Henzi and Barrett, 2002).

Despite the many studies on the social function of grooming we still have a partial and unclear picture of the topic. The contrasting results on the various benefits of grooming may have two, not mutually exclusive, explanations: one ecological/social and one methodological. The ecological/social explanation is that species live in different habitats and in different social groups (in terms of composition, organisation and size). These differences have to be taken into account when analysing the possible benefits of grooming. For animals inhabiting habitats where food is clumped, for example, it may be particularly beneficial to "buy" tolerance near food sources by grooming certain group members (i.e. high-ranking animals). This may be less important for species foraging on abundant or dispersed food sources. Under these ecological conditions animals may exchange grooming for other goods (e.g. infant handling) or for grooming itself. Habitat characteristics represent an important but sometimes neglected factor affecting social behaviour. For example, it is usually thought that folivores face low levels of direct food competition and thus have no particular need to establish amicable social relationships, because leaves are energetically poor, abundant and dispersed food sources. A recent study, however, has shown that leaves may sometimes occur in clumps and that, when this happens, food competition may be high (and so grooming may be used to obtain tolerance regarding access to food; Koenig *et al.*, 1998). This study exemplifies the difficulty in trying to generalise in biology: the benefits of grooming may be completely different for species/populations/social groups living under different ecological conditions.

This is particularly true for generalist species that usually occupy different ecological niches and have a wide geographical distribution (e.g. baboons; Henzi and Barrett, 2005).

The methodological explanation takes into account the fact that the benefits of grooming may represent rare events and that the cause-effect relationship between grooming and those events may be difficult to detect. Agonistic support, for example, is only, and not always, observable when some peculiar conditions are met. For example, taking for granted that grooming is of sufficient value to "buy" agonistic support (a statement still to be proven; e.g. Leinfelder *et al.*, 2001), grooming partners have to be close enough to quickly join forces against a third animal and, by doing so, they need to have a good chance of defeating the aggressor. The rarity of these events makes these studies difficult, particularly under field conditions, and requiring many hours of observations. Even when data from long-term studies are available, the problem is that grooming and social interactions among group members occur throughout the day, whereas behavioural observations are usually restricted to a relatively short time window (i.e. not more than 1 hour). It is thus difficult to prove a cause-effect relation between grooming exchange and its possible benefits (de Waal, 2003). This is the reason why studies usually tend to pool all the data together (as I did in Chapter 7) while not considering the temporal and sequential connection between grooming and, for example, agonistic support.

There are several unresolved issues regarding primate social relationships other than the lack of clear support for the relation between grooming and coalition formation. Some of these issues may be grouped into three main questions:

1) How are amicable social relationships established?

One of the problems for studies on grooming distribution is that they are usually restricted to a short period of time. That is, they analyse social relationships that are already established and rarely change during the course of the study. These studies thus are "snapshots" of the social relationship (Roberts and Sherratt, 1998), and cannot fully determine which strategies primates use to

avoid cheating and increase the sense of trust (Connor, 1995; Roberts and Sherratt, 1998). In order to analyse how social relationships are built, we need data collected while animals are in the process of establishing an amicable relationship (see Section 8.4 for possible situations).

2) How do we calculate the "value" of grooming?

We really do not know how much is the minimum amount of grooming "necessary" for an animal to exchange it with other goods or to consider its grooming partners as friends. This is a difficult, and maybe impossible, issue to deal with, as it requires some sort of "mind reading" and it raises serious risks of anthropomorphic explanations. Clearly, the amount of grooming given differs among animals and dyads, but we ignore to what extent economic laws apply to primate social behaviour (Noë *et al.*, 2001). In other words, we do not know if animals give grooming proportionately to the value of the good they want to obtain from their partners. Moreover, it is unclear how social relationships deteriorate when partners do not maintain stable grooming interactions (due, for example, to interference from other animals during grooming sessions). In captivity it would be possible to force two animals to progressively reduce each day the amount of grooming they exchange and to measure how this reduction affects, for example, tolerance regarding food sources. This experiment could help to explain if amicable relationships deteriorate gradually or if there is a minimum threshold of grooming to be exchanged, below which no benefits are obtained or social relationships switch from amicable to competitive.

3) What cognitive requirements are necessary to maintain social relationships?

Many experiments have been attempted to analyse the cognitive capacities of primate species. The results of these experiments indicate, according to some authors, that primates, and particularly apes, are capable of complex cognitive abilities and decision-making processes (e.g. Muroyama, 2002; van Schaik and Pradhan, 2003). Henzi and Barrett (1999) proposed that some characteristics of grooming distribution in primates (especially in monkeys) may be the results of

simple rules, not involving any complex cognitive ability. They suggest, for example, that the fact that in many species animals tend to direct their grooming towards high-ranking individuals may be explained by a simple rule of the thumb, such as "whenever possible groom the individual ranking higher than yourself". Therefore, according to this hypothesis, primates do not groom up the hierarchy because they "understand" that dominant individuals may potentially give them more benefits than low-ranking individuals. Contrasting this view is the observation that monkeys seem to be able to discriminate between kinship and social status (Bergman *et al.*, 2003). For example, baboons respond more intensely to playback calls mimicking rank reversal between families than within families, suggesting that they may classify group members according to their social status and kinship (similar playback experiments have also been carried out on vervet monkeys; Cheney & Seyfarth, 1990b). Such observations suggest the capacity of at least some primate species for complex cognitive abilities. At present, however, it is largely unclear if and how species-specific differences in cognitive abilities affect social relationships, the interchange of benefits, and cheating, although many studies have analysed social interactions at the dyadic level and using a game theoretic approach (Sherratt and Roberts, 2002). In animals with a good memory, for example, the time window between a grooming episode and its interchange for another good (e.g. agonistic support) may be extended. Conversely, an immediate interchange of benefits should be a more effective method to avoid cheating for species less able to remember past interactions.

8.3 Primate Social Relationships: Implications for Human Evolution and Psychology.

As happens in other research fields (e.g. medicine), the importance of studies on primate sociality as a means to increase our comprehension of human behaviour is widely recognised (e.g. Hinde, 1974). For example, by analysing the development of mother-infant interactions in non-human primates (mainly in the

rhesus macaque; Hinde, 1977; Hinde and Spencer-Booth, 1967), the importance of physical contact with their mothers for appropriate psychological development of human infants was fully recognised for the first time (Bowlby, 1971). Moreover, based on studies on reconciliation, the main mechanism used by non-human primates to manage conflicts (Aureli and de Waal, 2000; see Chapter 1), the ethological method was used to analyse peace-making mechanisms in human children (e.g. Ljungberg *et al.*, 1999). These studies showed that reconciliation occurs in a comparable way and is affected by similar factors in children and in non-human primates (particularly apes), despite their different cognitive capacities and physical development.

The evolutionary and comparative approach helps us to understand the similarities and differences between non-human primates and us. Even more important, it helps to comprehend the function of various behaviours. The possibility of understanding the ecological and social context in which a particular behavioural/psychological trait evolved is essential for studies on human evolution and psychology (e.g. Crawford, 1998; Daly and Wilson, 1999). Indeed, extant primates and primitive human societies are the best research tool we possess to study the relationship between ecology, social behaviour and brain evolution in early humans. For example, the genus *Papio* represents an ideal model for analysing the importance of the ecological context for the evolution of the first hominids, as *Papio* and *Homo* both appeared when climatic changes led to the emergence of the African savannah (Henzi and Barrett, 2005).

There is now convincing evidence that a positive relationship exists between the average group size of each social species and brain size or, more correctly, neocortex size, when controlling for body size. This relationship has been found in primates (both humans and non-humans) and, partially, in carnivores and insectivores (Barton, 1996; Dunbar, 1996, 2003a, b; Dunbar and Beaver, 1998). Originally, the evolution of human intellectual abilities was thought to be related to the need to solve ecological problems (e.g. foraging on food requiring extractive skills) and to be associated with cooperative hunting and tool use (Jerison, 1973). However, Byrne and Whiten (1988) suggested an alternative hypothesis, stating that the necessity to survive in a complex social environment

was at the root of the increase of the neocortex (the social brain hypothesis). This hypothesis assumes the following evolutionary pathway (Dunbar, 2003b): group living evolved in ancestral primates as a means to reduce predation risk. With the emergence of the African savannah, some ancestral primate species are thought to have begun to spend increasing and significant proportions of their time on the ground and in open habitats. For these species, the benefits of living in larger groups were greater than for arboreal/forest species. Larger groups, in turn, represented more complex social environments where good coordination of movements and activities among the various group members is essential to maintain coherent social units. Group-living also represents an opportunity for additional benefits, some of them being obtained through the formation of social bonds with other group members. We may hypothesise that social relationships (particularly with kin) gave many benefits to group members by increasing cooperative or altruistic acts such as predator mobbing, food sharing, coalition formation and cooperative hunting. Under these conditions, larger neocortices were favoured during the course of evolution. Larger neocortices, and the increased cognitive capacity that this permitted, were necessary for each group member to maintain stable and long-lasting amicable relationships, to recognise each group companion, to memorise past interactions with the other animals or among third individuals, and to integrate the various individuals into its mental social world (Dunbar, 2003b).

Supporting the importance of the evolutionary and comparative approach, regression analyses using data on the neocortex size of living primates and empirical studies agree in their calculation of the maximum number of people with whom each of us is able to maintain personal relationships (as opposed to impersonal or formal relationships), that is, approximately 150 individuals. Interestingly, this figure is in between two social units of primordial human societies (Hill and Dunbar, 2002): the overnight camps of foraging people (usually formed by 30-40 people) and the tribal units (i.e. 1500-2000 people). The progressive increase in group size began to rise exponentially from around one million years ago, during the *Homo erectus* period. It was this increase in group size that clearly distinguished the grouping patterns of early humans from those of

apes, although we still cannot definitely say whether this increase was the cause or the effect of the neocortex enlargement. Individuals living in larger groups not only required greater cognitive abilities to cope with this complex social environment but also a more effective means to maintain social bonds and to exchange information (about, for example, the location of food) with the other group companions (Dunbar, 2003b). Indeed, the larger the group, the greater the amount of time that group members have to devote to foraging activities (as food depletion rate for a given area increases proportionately with group size) at the expenses of other activities (e.g. grooming). Moreover, grooming is a time-consuming task and a behaviour that cannot be given to more than one partner at a time. This is also true for the human equivalents of grooming, such as cuddling and petting (Eibl-Eiblsfeldt, 1993). In this context and to respond to such social needs, at a certain point in the course of human evolution (probably around 1.0-0.5 million years ago; Tattersall, 1998) morphological changes in the larynx allowed hominids to produce complex sounds that eventually evolved into a proper language. Language is much more effective than grooming in maintaining group cohesion and amicable social relationships, and for information exchange, for four main reasons (Dunbar, 1998). First, it makes it possible to interact with many individuals at the same time. Second, it is possible to speak while being engaged in something else (e.g. foraging) whereas grooming is basically an exclusive activity. Third, linguistic exchange does not require close proximity between two individuals and thus it allows effective group cohesion and coordination of movements. Fourth, and related to the previous point, language allows us to obtain information about events that happened during our absence, and it may convey detailed information, for example, on the exact location of food. Language thus allowed early humans to live in larger social groups and to cooperate in more complex ways. Non-human primates and other animals do use vocal communication for various purposes, such contact calls to maintain inter-individual proximity or food calls to inform other group members about a particularly rich food source (Hauser, 1996). This type of vocal behaviour, however, is not at all comparable to the complexity of human language. This complexity is at the base of the evolution and diversification oh human cultures.

The evolutionary approach is also useful for our comprehension of human social relationships in modern societies. Modern Western societies represent environments largely different from those of our ancestors. Among other important differences, men and women in Western societies may, or have to, interact on a regular basis with many more people than those forming the average social unit in primitive human societies (e.g. Eibl-Eiblsfeldt, 1993). The sense of frustration that many modern people experience resulting from the inability (due, for example, to time constraints) to maintain many stable social relationships or the tendency to limit the number of such relationships may be explained using an evolutionary approach. We may now thus face the challenge of living in societies where social relationships with many people are possible, if not necessary, whereas time and cognitive constraints impose a limit on the number of such relationships.

The results of this Thesis broadly support all these considerations. Indeed, group size was the main, if not the only, factor among the various factors considered (e.g. season and ambient temperature) to have a significant effect on grooming distribution in the two groups of Japanese macaques studied (see Chapter 6). This is important in light of the fact that studies using an evolutionary approach have usually focused their attention more on the effect of habitat characteristics (e.g. vegetation type) on the evolution of social relationships than on the social environment (e.g. van Schaik, 1989). It is possible that, in areas where primates face high food abundance and no predation risk, as on Yakushima island, habitat characteristics have a milder effect on social behaviour than group size. Indeed, we may hypothesise that, with the progressively increased control that early humans had on the environment, the role of ecological factors in shaping social patterns decreased at the expense of the social context.

8.4 Possible Lines of Future Research on Grooming Distribution.

Behavioural studies ideally need long-term data in order to properly address the topic they aim to analyse. This is particularly true for studies conducted in the

field, where logistic conditions may limit the amount of data collected each day, and those analysing rare events, such as coalition formation (see above). For example, the complex patterns of grouping behaviour and the social relationships among African elephants would not have been clear without long-term data from the field (Moss, 1988). This Thesis has, however, presented a thorough account of some of the factors that may affect grooming distribution in the Japanese macaque. As such, it may potentially represent a starting point for methodological improvements, new ideas and analyses.

The first weakness of this study was that I was unable to obtain information on the genetic relationships between the females belonging to the larger group (i.e. Kw group, see Chapter 2).Although, I collected faecal samples from the females in Kw group (the genetic relationship of Nina A females was already known at the start of my study), these samples have not been analysed due to difficulties in extracting and analysing DNA from faecal samples as well as to the high costs of such analyses. Second, if feasible I would try to increase the length of my focal sessions, which only lasted 10 minutes (see Chapter 2). This time window was chosen following a preliminary study conducted before the start of my data collection, in May 2001 (see Chapter 2), when I found that longer observation sessions (e.g. 20 minutes) would have significantly increased the chances of losing the focal animal during the session. With a data collection period longer than one year, the benefits of longer focal sessions would have counterbalanced interrupted sessions. At the same time, however, this procedure would have biased the sample. Monkeys who spent a longer consecutive period of time engaged in one activity (e.g. grooming) would never have been lost whereas this would have frequently happened for monkeys who often switch from one activity to the other. Important data would thus have potentially been lost on the latter monkeys. Whether or not this would have happened, it is clear that longer focal sessions would have allowed me to analyse more effectively the method used by Barrett and colleagues (1999) to measure grooming reciprocation, as more complete grooming interactions would have been recorded (see Chapter 4). The final consideration with respect to this topic is that field studies are always forced to be a compromise between the ideal way to tackle a research theme and what it is

really possible to do with wild animals. Field studies may be less rigorous than laboratory experiments, where variables may be better controlled, but they may give a better insight into what animals are really "supposed to do" in their environment (Yamagiwa and Hill, 1998).

Having data collected over a number of years and on various troops of different size and composition would allow more detailed analyses on the factors affecting grooming distribution. Although seasonal changes in activity budgets had no effect on grooming in this study (see Chapter 5), this may not be true for all years or for other groups. The coastal forest of Yakushima island is a fairly stable and rich habitat, and indeed differences in diet composition and activity across the seasons were relatively mild. Some dramatic periods of food shortage have, however, been documented in Yakushima (Hanya *et al.*, 2004). It is thus possible that during those periods, food competition and time constraints on grooming are greater than they were during the course of this study, and under those conditions seasonal changes in grooming distribution might become evident. The effect of periodic or unpredictable changes in food abundance or distribution may interplay with group size. We may hypothesise that these periods of food shortage have stronger effects on grooming distribution the larger the group is, given that larger groups are less socially stable (see Chapter 6), making them potentially more sensitive to variations in food availability. Also, a larger data set would help to understand how, and to what extent, grooming distribution varies in relation to group size. With data on only two groups, it is impossible to determine what is the maximum amount of time that animals may devote to grooming with respect of the size of their group and other things being equal (e.g. habitat productivity). Furthermore, long-term data would be particularly beneficial for detailed analyses of rare events. For example, the importance of coalition formation against female aggressors in Nina A group could not be determined (see Chapters 5 and 7) because of their rarity, but this could be analysed with longer-term data and data on more study groups. This would also make it possible to analyse the effect of two additional factors on grooming distribution, namely, between-group direct food competition and operational sex ratio (OSR; see Table 1.1 for a definition). It has frequently been proposed that social relationships

among females should be tighter and more cohesive under high levels of between-group food competition (e.g. Sterck *et al.*, 1997). Cohesive relationships are though to favour cooperative defence of food sources and thus to increase access to those resources. This prediction, however, has been rarely tested, and when analysed, it has not been supported by empirical data (e.g. Cheney, 1992). The OSR of a group and the type of interactions between the two sexes may both affect female social relationships (Nunn, 1999; Nunn and van Schaik, 2000), although the importance of these factors has often been neglected. The effect of inter-group food competition and of OSR could be properly tested using data collected on groups of different composition and facing different level of inter-group competition.

Although this Thesis showed that a positive relationship exists between amount of grooming exchanged between two females and tolerance around food sources, this point needs more fine-tuned analyses. By collecting data on a female macaque for a longer period of time (e.g. 5 hours) and after a grooming session with another monkey, for example, it could be possible to determine if grooming increases the likelihood that two partners forage on the same food patch on a short-time scale. Indeed, sequential analysis would be particularly beneficial for studies on the relationship between grooming and tolerance. Possible problems with this type of analysis, however, are the difficulty in following the monkeys for a long period of time, due to the steepness of the study area (see above and Chapter 2). Moreover, the fact that Yakushima macaques usually exchange grooming with many group females during the same grooming session, may present a confounding factor. That is, grooming may promote co-feeding, but a monkey may "prefer" to forage on the same food patch with one of her previous grooming partners and not with another for various reasons. For example, the decision to join a particular grooming partner may be based on the size of the patch on which the partners are foraging. The possibility of finding evidence for a cause-effect link between grooming and tolerance may thus depend on the grooming partner (among the several that a monkey had during the grooming session) on whom the observer decides to focus attention.

One final issue I would like to analyse in the near future concerns the strategy (e.g. the "raise the stakes" strategy; see Chapter 1) that animals use to avoid cheating and to increase the sense of trust in their partners when they are establishing (or re-establishing) an amicable social relationship. One possibility would be to collect data on juvenile primates when they begin to become independent from their mothers and to establish grooming relationships with other group members. Moreover, it would be interesting to analyse grooming interactions among individuals who have previously had an aggressive interaction. If conflicts do damage previously amicable relationships (Koyama, 2001) then reconciliation is the moment when such relationships are re-established. Conversely, grooming interactions between group members represent a "snap-shot" of such relationships (see above) and they cannot properly test the various strategies of grooming exchange. Therefore, the analysis of the first grooming interactions between two individuals after a conflict may help to clarify which strategy monkeys use to build amicable relationships.

REFERENCES

Agetsuma N. (1995a). Foraging strategies of Yakushima macaques (*Macaca fuscata yakui*). *International Journal of Primatology*, 16: 595-610.

Agetsuma N. (1995b). Dietary selection by Yakushima macaques (*Macaca fuscata yakui*): the influence of food availability and temperature. *International Journal of Primatology*, 16: 611-627.

Agetsuma N. (1998). Effects of habitat differences on feeding behaviors of Japanese monkeys: comparison between Yakushima and Kinkazan. *Primates*, 39: 275-289.

Agetsuma N., Sugiura H., Hill D.A., Agetsuma-Yanagihara Y. and Tanaka T. (2003). Population density and group composition of Japanese sika deer (*Cervus nippon yakushimae*) in an evergreen broad-leaved forest in Yakushima, southern Japan. *Ecological Research*, 18: 475-483.

Alexander B.K. and Bowers J.M. (1967). The social structure of the Oregon troop of Japanese macaques. *Primates*, 8: 333-340.

Altmann J. (1974). Observational study of behavior: sampling methods. *Behaviour*, 49: 227-267.

Altmann J. (1980). *Baboon Mothers and Infants*. Harvard University Press, Cambridge, U.S.A.

Arnold K. and Whiten A. (2003). Grooming interactions among the chimpanzees of the Budongo forest, Uganda: Tests of five explanatory models. *Behaviour*, 140: 519-552.

Aureli F. and de Waal F.B.M. (2000). *Natural Conflict Resolution*. University of California Press, Berkeley, U.S.A.

Aureli F. and van Schaik C.P. (1991). Post-conflict behaviour in long-tailed macaques (*Macaca fascicularis*): I. Coping with the uncertainty. *Ethology*, 89: 101-114.

Aureli F., Das M. and Veenema H.C. (1997). Differential kinship effect on reconciliation in three species of macaques (*Macaca fascicularis*, *M. fuscata*, and *M. sylvanus*). *Journal of Comparative Psychology*, 111: 91-99.

Aureli F., Cords M. and van Schaik C.P. (2002). Conflict resolution following aggression in gregarious animals: a predictive framework. *Animal Behaviour*, 64: 325-343.

Axelrod R. and Hamilton W.D. (1981). The evolution of cooperation. *Science* 211: 1390-1396.

Axén A.H. and Pierce N.E. (1998). Aggregation as a cost-reducing strategy for lycaenid larvae. *Behavioral Ecology*, 9: 109-115.

Axén A.H., Leimar O. and Hoffmann V. (1996). Signalling in a mutualistic interaction. *Animal Behaviour*, 52: 321-333.

Barton R. (1985). Grooming site preferences in primates and their functional implications. *International Journal of Primatology*, 6: 519-532.

Barrett L. and Henzi S.P. (2001). The utility of grooming in baboon troops. In: Noë R., van Hooff J.A.R.A.M. and Hammerstein P. (Eds.), *Economics in Nature*, pp. 119-145. Cambridge University Press, Cambridge, U.K.

Barrett L. and Henzi S.P. (2002). Constraints on relationship formation among female primates. *Behaviour*, 139: 263-289.

Barrett L., Henzi S.P., Weingrill T., Lycett J.E. and Hill R.A. (1999). Market forces predict grooming reciprocity in female baboons. *Proceedings of the Royal Society of London, B Series*, 266: 665-670.

Barrett L., Henzi S.P., Weingrill T., Lycett J.E. and Hill R.A. (2000). Female baboons give as good as they get, but do not raise the stakes. *Animal Behaviour*, 59: 763-770.

Barrett L., Gaynor D. and Henzi S.P. (2002a). A dynamic interaction between aggression and grooming reciprocity among female chacma baboons. *Animal Behaviour*, 63: 1047-1053.

Barrett L., Dunbar R.I.M. and Lycett J. (2002b). *Human Evolutionary Psychology*. Palgrave, New York, U.S.A.

Barton R. (1985). Grooming site preferences in primates and their functional implications. *International Journal of Primatology*, 6: 519-532.

Barton R.A. (1996). Neocortex size and the behavioural ecology in primates. *Proceedings of the Royal Society of London, B Series*, 263: 173-177.

Barton R.A. and Dunbar R.I.M. (1997). Evolution of the social brain. In: Whiten A. and Byrne R. (Eds.), *Machiavellian Intelligence II*, pp. 240-263. Cambridge University Press, Cambridge, U.K.

Barton R.A., Byrne R.W. and Whiten A. (1996). Ecology, feeding competition and social structure in baboons. *Behavioral Ecology and Sociobiology*, 38: 321-329.

Bearder S. K. (1987). Lorises, bushbabies, and tarsiers: diverse societies in solitary foragers. In: Smuts B.B., Cheney D.L., Seyfarth R.M., Wrangham R.W. and Struhsaker T.T. (Eds.), *Primate Societies*, pp. 11-24. University of Chicago Press, Chicago, U.S.A.

Belisle P. and Chapais B. (2001). Tolerated co-feeding in relation to degree of kinship in Japanese macaques. *Behaviour*, 138: 487-509.

Bergman T.J., Beenher J.C., Cheney D.L. and Seyfarth R.M. (2003). Hierarchical classification by rank and kinship in baboons. *Science*, 302: 1234-1236.

Bernstein I.S. (1972). Daily activity cycles and weather influences on a pigtail monkey group. *Folia Primatologica*, 18: 390-415.

Bernstein I.S. (1980). Activity patterns in a stumptail macaque group (*Macaca arctoides*). *Folia Primatologica*, 33: 20-45.

Bernstein I.S. and Mason W.A. (1963). Activity patterns of rhesus monkeys in a social group. *Animal Behaviour*, 11: 455-460.

Bicca-Marques J.C. and Calegaro-Marques C. (1998). Behavioural thermoregulation in a sexually and developmentally dichromatic Neotropical primate, the black-and-gold howling monkey (*Alouatta caraya*). *American Journal of Physical Anthropology*, 106: 533-546.

Blaffer-Hrdy S. (1979). Infanticide among animals: a review, classification, and examination of the implications for the reproductive strategies of females. *Ethology and Sociobiology*, 1: 13-40.

Boccia M. L. (1983). A functional analysis of social grooming through direct comparison with self-grooming in rhesus monkeys. *International Journal of Primatology*, 4: 399-418.

Boccia M.L. (1987). The physiology of grooming: a test of the tension reduction hypothesis. *American Journal of Primatology*,12: 330.

Boccia M.L., Rockwood B. and Novak M. (1982). The influence of behavioral context and social characteristics on the physical aspects of social grooming in rhesus monkeys. *International Journal of Primatology*, 3: 91-108.

Boccia M.L., Reite M. and Laudenslager M. (1989). On the physiology of grooming in a pigtail macaque. *Physiology and Behavior,* 45: 667-670.

Bowlby J. (1971). *Attachment and Loss. I. Attachment.* Penguin Books, New York, U.S.A.

Brent L., Koban T. and Evans S. (2003). The influence of temperature on the behavior of captive mother-infant baboons. *Behaviour*, 140: 209-224.

Bshary R. (2001). The cleaner fish market. In: Noë R., van Hooff J.A.R.A.M. and Hammerstein P. (Eds.), *Economics in Nature*, pp. 146-172. Oxford University Press, U.K.

Byrne R. and Whiten A. (1988), *Machiavellian Intelligence.* Cambridge University Press, Cambridge, U.K.

Calhoun J.B.(1962). Population density and social pathology. *Scientific American*, 206: 139-148.

Call J., Judge P. and de Waal F.B.M. (1996). Influence of kinship and spatial density on reconciliation and grooming in rhesus monkeys. *American Journal of Primatology*, 39:35-45.

Carpenter C.R. (1942). Sexual behavior of free-ranging rhesus monkeys (*Macaca mulatta*). *Journal of Comparative Psychology*, 33: 113-162.

Castles D.L., Aureli F. and de Waal F.B.M. (1996). Variation in conciliatory tendecy and relationship quality across groups of pigtail macaques. *Animal Behaviour*, 52: 389-403.

Chaffin C.L., Friedlen K., de Waal F.B.M. (1995). Dominance style of Japanese macaques compared with rhesus and stumptail macaques. *American Journal of Primatology*, 35: 103-116.

Chapais B., Girard M. and Primi G. (1991). Non-kin alliances and the stability of matrilineal dominance relations in Japanese macaques. *Animal Behaviour*, 41: 481-491.

Chapais B, Gauthier C. and Prud'homme J. (1995). Dominance competition through affiliation and support in Japanese macaques: an experimental study. *International Journal of Primatology*, 16: 521-536.

Cheney D.L. (1981). Intergroup encounters among free-ranging vervet monkeys. *Folia Primatologica*, 35: 124-146.

Cheney D.L. (1992). Intragroup cohesion and intergroup hostility: the relation between grooming distributions and intergroup competition among female primates. *Behavioral Ecology*, 3: 334-345.

Cheney D.L. and Seyfarth R.M. (1990a). The recognition of social alliances by vervet monkeys. *Animal Behaviour*, 34: 1722-1731.

Cheney DL and Seyfarth R.M. (1990b). *How Monkeys See the World.* University of Chicago Press, Chicago, U.S.A.

Cheney D.L. and Seyfarth R.M. (1999). Recognition of other individuals' social relationships by female baboons. *Animal Behaviour*, 58: 67-75.

Cheney D.L., Seyfarth R.M., Fischer J., Beehner J., Bergman T., Johnson S.E., Kitchen D.M., Palombit R.A., Rendall D., and Silk J.B. (2004). Factors affecting Reproduction and mortality among baboons in the Okavango Delta, Botswana. *International Journal of Primatology*, 25: 401-427.

Chism J. and Rogers W. (2003). Grooming and social cohesion in patas monkeys and other guenons. In: Glenn M.E. and Cords M. (Eds.), *The Guenons, Diversity and Adaptation in African Monkeys*, pp. 232-244. Kluwer Academic, New York, U.S.A.

Clutton-Brock T.H. and Harvey P.H. (1976). Evolutionary rules and primate societies. In: Bateson P.P.G. and Hinde R.A. (Eds.), *Growing Points in Ethology*, pp. 195-237. Cambridge University Press, Cambridge, U.K.

Clutton-Brock T.H. and Harvey P.H. (1977). Primate ecology and social organization. *Journal of Zoology*, 183: 1-39.

Coelho A., Turner S. and Bramblett C. (1983). Allogrooming and social status: an assessment of the contributions of female behavior to the social organization of hamadryas baboons (*Papio hamadryas*). *Primates*, 24: 184-197.

Connor R.C. (1995). Impala allogrooming and the parcelling model of reciprocity. *Animal Behaviour* 49: 528-530.

Conradt L., Clutton-Brock T.H. and Guinness F.E. (2000). Sex differences in weather sensitivity can cause habitat segregation: red deer as an example. *Animal Behaviour*, 59: 1049-1060.

Cooper M.A. and Bernstein I.S. (2000). Social grooming in Assamese macaques (*Macaca assamensis*). *American Journal of Primatology*, 50: 77-85.

Cords M. (1992) Post-conflict reunions and reconciliation in long-tailed macaques. *Animal Behaviour*, 44:57–61

Cords M. (1995). Predator vigilance costs of allogrooming in wild blue monkeys. *Behaviour*, 132: 559-569.

Cords M. (1997). Friendships, alliances, reciprocity and repair. In: Whiten A. and Byrne R. (Eds.), *Machiavellian Intelligence II*, pp. 24-49. Cambridge University Press, Cambridge, U.K

Cords M. (2000). Grooming partners of immature blue monkeys (*Cercopithecus mitis*) in the Kakamega forest, Kenya. *International Journal of Primatology,* 21: 239-254.

Cords M. (2001). Friendship among adult female blue monkeys (*Cercopithecus mitis*). *Behaviour*, 139: 291-314.

Cords M. and Thurnheer S. (1993). Reconciling with valuable partners by long-tailed macaques. *Ethology*, 93: 315-325.

Cords M. and Aureli F. (1996). Reasons for reconciling. *Evolutionary Anthropology*, 5: 42-45.

Cords M. and Aureli F. (2000). Reconciliation and relationship qualities. In: Aureli F. and de Waal F.B.M. (Eds.), *Natural Conflict Resolution*, pp. 177-198. University of California Press, Berkeley, CA, U.S.A.

Crawford C. (1998). Environments and adaptations: then and now. In: Crawford C. and Krebs D.L. (Eds.), *Handbook of Evolutionary Psychology*, pp. 275–302. Lawrence Erlbaum, Mahwah, U.S.A.

Crook J.H. and Gartlan J.S. (1966). Evolution of primate societies. *Nature*, 210: 1200-1203.

Dahl J.F. and Smith E.O. (1985). Assessing variation in the social behavior of stumptail macaques using thermal criteria. *American Journal of Physical Anthropology*, 68: 467-477.

Dahl J.F., Bernstein I.S. and Williams L.E. (1986). Thermoregulation and social structure of a captive group of rhesus macaques. In: Taub D.M. and King F.A. (Eds.), *Current Perspectives in Primate Social Dynamics*, p 243-251. van Nostrand Reinhold, New York, U.S.A.

D'Amato F.R., Troisi A., Scucchi S. and Fuccillo R. (1982). Mating season influence on allogrooming in a confined group of Japanese macaques: a quantitative analysis. *Primates*, 23: 220-232.

Daly M. and Wilson M.I. (1999). Human evolutionary psychology and animal behaviour. *Animal Behaviour*, 57: 509-519.

Dasilva G.L. (1993). Postural changes and behavioural thermoregulation in *Colobus polykomos* – the effect of climate and diet. *African Journal of Ecology*, 31: 226-241.

Dasser V. (1988). A social concept in Java monkeys. *Animal Behaviour*, 36: 225-230.

Datta S.B. (1988). The acquisition of dominance among free-ranging rhesus monkey siblings. *Animal Behaviour*, 36: 754-772.

Defler T.R. (1978). Allogrooming in two species of macaque (*Macaca nemestrina* and *Macaca radiata*). *Primates*, 19: 153-167.

De Vries H. (1993). The rowwise correlation between two proximity matrices and the parcial rowwise correlation. *Psychometrika*, 58: 53-69.

de Waal F.B.M. (1977). The organization of agonistic relations within two groups of Java-monkeys (*Macaca fascicularis*). *Zeitchrift fur Tierpsychologie*, 44: 225-282.

de Waal F.B.M. (1986). Class structure in a rhesus monkey group: the interplay between dominance and tolerance. *Animal Behaviour*, 34: 1033-1040.

de Waal F.B.M. (1989). Food sharing and reciprocal obligations among chimpanzees. *Journal of Human Evolution*, 18: 433-459.

de Waal F.B.M. (1991). Rank distance as a central feature of rhesus monkey social organization: a sociometric analysis. *Animal Behaviour*, 41: 383-396.

de Waal F.B.M. (1992). Coalition as part of reciprocal relations in the Arnheim chimpanzees colony. In: Harcourt A.H. and de Waal F.B.M. (Eds.),

Coalitions and Alliances in Humans and Other Animals, pp. 233-258. Oxford University Press, Oxford, U.K.

de Waal F.B.M. (1997). The chimpanzee's service economy: food for grooming. *Evolution and Human Behavior,* 18: 375-386.

de Waal F.B.M. (2003). Social syntax: The if-then structure of social problem solving. In: de Waal F.B.M. and Tyack P.L. (Eds.), *Animal Social Complexity. Intelligence, Culture, and Individualizes Societies*, pp. 230-248. Harvard University Press, Cambridge, MA, U.S.A.

de Waal F.B.M. and Hoekstra J.A. (1980). Contexts and predictability of aggression in chimpanzees. *Animal Behaviour*, 28: 929-937.

de Waal F.B.M. and van Roosmalen A. (1979). Reconciliation and consolation among chimpanzees. *Behavioral Ecology and Sociobiology,* 5: 55-66.

de Waal F.B.M and Luttrell L.M. (1986). The similarity principle underlying social bonding among female rhesus monkeys. *Folia Primatologica*, 46: 215-234.

de Waal F.B.M, Luttrell L.M. (1988). Mechanisms of social reciprocity in three primate species: symmetrical relationship characteristics of cognition. *Behavioral Ecology and Sociobiology*. 9: 101-118.

de Waal F.B.M and Tyack P.L. (2003). *Animal Social Complexity*. Cambridge University Press, Harvard, USA.

Di Bitetti M.S. (1997). Evidence for an important social role of allogrooming in a platyrrhine primate. *Animal Behaviour*, 54: 199-211.

Di Bitetti M.S. 2000. The distribution of grooming among female primates: testing hypotheses with the Shannon-Wiener diversity index. *Behaviour*, 137: 1517-1540.

Digby L.J. (1995). Infant care, infanticide, and female reproductive strategies in polygynous groups of common marmosets (*Callithrix jacchus*). *Behavioral Ecology and Sociobiology,* 37:51-61.

Dunbar R.I.M. (1983). Structure of gelada baboon reproductive units. II. Social relationships between reproductive females. *Animal Behaviour*, 31:556-564.

Dunbar R.I.M. (1984). *Reproductive Decisions: an Economic Analysis of the Gelada Baboon Social System*. Princeton University Press, Princeton, U.S.A.

Dunbar R.I.M. (1988). *Primate Social Systems.* Cornell University Press, Ithaca, New York, U.S.A.

Dunbar R.I.M. (1991). Functional significance of social grooming in primates. *Folia Primatologica,* 57: 121-131.

Dunbar R.I.M. (1992). Time: a hidden constraint on the behavioural ecology of baboons. *Behavioral Ecology and Sociobiology*, 31: 35-49.

Dunbar R.I.M. (1996). Determinants of group size in primates: a general model. *Proceedings of the British Academy*, 88: 33-57.

Dunbar R.I.M. (1998). *Dalla nascita del linguaggio alla babele delle lingue.* Longanesi and C., Milan, Italy.

Dunbar R.I.M. (2002). Modelling primate behavioural ecology. *International Journal of Primatology*, 23: 785-819.

Dunbar R.I.M. (2003a). Evolution of the social brain. *Science*, 302: 1160-1161.

Dunbar R.I.M. (2003b). The social brain: Mind, language, and society in evolutionary perspective. *Annual Review of Anthropology*, 32: 163-181.

Dunbar R.I.M. and Beaver J. (1998). Neocortex size predicts group size in carnivores and some insectivores. *Ethology*, 104: 695-708.

Dunbar R.I.M. and Dunbar P. (1988). Maternal time budgets in gelada baboons. *Animal Behaviour*, 36: 970-980.

Dunbar R.I.M. and Sharman M. (1984). Is social grooming altruistic? *Zeitschrift für Tierpsychologie*, 64: 163-173.

Eibl-Eiblsfeldt I. (1993). *Etologia Umana.* Bollati Boringhieri, Turin, Italy.

Everitt B.S. (1996). *Making Sense of Statistics in Psychology.* Oxford University Press, Oxford, U.K.

Fairbanks L. 1980. Relationships among adult females in captive vervet monkeys: testing a model of rank-related attractiveness. *Animal Behaviour*, 28: 853-859.

Fairbanks L. and Bird J. (1978). Ecological correlates of interindividual distance in the St. Kitts vervet (*Cercopithecus aethiops sabaeus*). *Primates*, 19: 605-614.

Feh C. and de Mazieres J. (1993). Grooming at a preferred site reduces heart rate in horses. *Animal Behaviour*, 46: 1191-1194.

Fleagle J.G. (1999). *Primate Adaptation and Evolution*. Academic Press, San Diego, U.S.A.

Freeland W.J. (1981). Functional aspects of primate grooming. *Ohio Journal of Science*, 81: 173-177.

Furuichi T. (1983). Interindividual distance and influence of dominance on feeding in a natural Japanese macaques troop. *Primates*, 24: 445-455.

Goodall J. (1986). *The Chimpanzees of Gombe. Patterns of Behavior*. Belknap Press, Cambridge, MA, U.S.A.

Gould J.L. (1982). Why do honeybees have dialects? *Behavioral Ecology and Sociobiology*, 10: 53-56.

Gygax L., Nerida H., Kummer H. (1997). A matrilineal overthrow with destructive aggression in *Macaca fascicularis*. *Primates*. 38: 149-158.

Hamilton W.D. (1964). The genetical evolution of social behavior. I and II. *Journal of Theoretical Biology*, 7: 1-52.

Hamilton W.D. (1971). Geometry of the selfish herd. *Journal of Theoretical Biology*, 31: 295-311.

Hanby J.P. and Brown C.E. 1974. The development of sociosexual behaviours in Japanese macaques *Macaca fuscata. Behaviour*, 59: 152-196.

Hanya G., Noma N. and Agetsuma N. (2003). Altitudinal and seasonal variations in the diet of Japanese macaques in Yakushima. *Primates*, 44: 51-59.

Hanya G., Matsubara M., Sugiura H., Hayakawa S., Goto S., Tanaka T., Soltis J. and Noma N. (2004). Mass mortality of Japanese macaques in a western coastal forest of Yakushima. *Ecological Research*, 19: 179–188

Harcourt A. (1992). Coalitions and alliances: are primates more complex than non-primates? In: Harcourt A.H. and de Waal F.B.M. (Eds.), *Coalitions and Alliances in Humans and Other Animals*, pp. 445-472. Oxford University Press, Oxford, U.K.

Harcourt A.H. and de Waal F.B.M. (1992). *Coalitions and Alliances in Humans and Other Animals*. Oxford University Press, Oxford, U.K.

Harrison M.J.S. (1985). Time budget of the green monkey, *Cercopithecus sabaeus*: some optimal strategies. *International Journal of Primatology*, 6: 351-376.

Hart B.L. (1990). Behavioral adaptation to pathogens and parasites: five strategies. *Neuroscience and Biobehavioral Reviews*, 14: 273-294.

Hart B.L. and Hart L.A. (1992). Reciprocal allogrooming in impala (*Aepyceros melampus*). *Animal Behaviour*, 44: 1073-1083.

Hauser M.D. (1996). *The Evolution of Communication*. MIT Press, Massachusetts, U.S.A.

Heiduck S. (2002). The use of undisturbed forest by masked titi monkeys *Callicebus personatus melanochir* is proportional to food availability. *Oryx*, 36: 133-139.

Hemelrijk C. (1990). A matrix partial correlation test used in investigations of reciprocity and other social interaction patterns at group level. *Journal of Theoretical Biology*, 143: 405-420.

Hemelrijk C. (1994). Support for being groomed in long-tailed macaques, *Macaca fascicularis*. *Animal Behaviour*, 48: 479-481.

Hemelrijk C. and Ek A. (1991). Reciprocity and interchange of grooming and "support" in captive chimpanzees. *Animal Behaviour*, 41: 923-935.

Hemelrijk C. and Luteijn M. (1998). Philopatry, male presence and grooming reciprocation among female primates: a comparative perspective. *Behavioral Ecology and Sociobiology*, 42: 207-215.

Hemelrijk C.K., van Laere G.J., van Hooff J.A.R.A.M. (1992). Sexual exchange relationships in captive chimpanzees? *Behavioral Ecology and Sociobiology*, 30: 269-275.

Henzi S.P. and Barrett L. (1999). The value of grooming to female primates. *Primates*, 40: 47-59.

Henzi S.P. and Barrett L. (2002). Infants as a commodity in a baboon market. *Animal Behaviour*, 63: 915-921.

Henzi S.P. and Barrett L. (2005). The historical socioecology of savana baboons (*Papio hamadryas*). *Journal of Zoology*, 265: 215-226.

Henzi S.P., Lycett J.E. and Weingrill T. (1997). Cohort size and the allocation of social effort by female mountain baboons. *Animal Behaviour*, 54: 1235-1243.

Henzi S.P., Barrett L., Gaynor D., Greeff J., Weingrill T. and Hill R.A. (2003). Effect of resource competition on the long-term allocation of grooming by

female baboons: evaluating Seyfarth's model. *Animal Behaviour*, 66: 931-938.

Hill D.A. (1997). Seasonal variation in the feeding behavior and diet of Japanese macaques (*Macaca fuscata yakui*) in lowland forest of Yakushima. *American Journal of Primatology*, 43: 305-322.

Hill D.A. and Okayasu N. (1996). Determinants of dominance among female macaques: nepotism, demography, and danger. In: Fa J.E. and Lindburg D.G. (Eds.), *Evolution and Ecology of Macaque Societies*, pp. 459-472. Cambridge University Press, Cambridge, U.K.

Hill R.A. and Dunbar R.I.M. (1998). An evaluation of the roles of predation rate and predation risk as selective pressures on primate grouping behaviour. *Behaviour*, 135(4): 411-430.

Hill R.A. and Dunbar R.I.M. (2002). Social network size in humans. *Human Nature*, 14: 53-72.

Hill R.A., Weingrill T., Barrett L. and Henzi S.P. (2004). Indices of environmental temperatures for primates in open habitats. *Primates*, 45: 7-13.

Hinde R.A. (1974). *Biological Bases of Human Social Behaviour*. McGraw-Hill, U.K.

Hinde R.A. (1976). Interactions, relationships, and social structure. *Man*, 11: 1-17.

Hinde R.A. (1977). Mother-infant separation and the nature of interindividual relationships: experiments with rhesus monkeys. *Proceedings of the Royal Society of London, B Series*, 196: 29-50.

Hinde R.A. and Spencer-Booth Y. (1967). The behaviour of socially living rhesus monkeys in their first two and a half years. *Animal Behaviour*, 15: 169-196.

Hoage R.J. (1978). Parental care in *Leontopithecus rosalia rosalia*: sex and age differences in carrying behaviour and the role of prior experience. In: Kleiman D.G. (Ed.), *The Biology and Conservation of the Callitrichidae*, pp. 293-305. Smithsonian Institution Press, Washington, U.S.A.

Howell D.C. (1999). *Fundamental Statistics for the Behavioral Sciences*. Duxbury Press, Belmont, U.S.A.

Hutchins M. and Barash D.P. (1976). Grooming in primates: implications for its utilitarian function. *Primates*, 17: 145-150.

Ihobe H. (1989). How social relationships influence a monkey's choice of feeding sites in the troop of Japanese macaques (*Macaca fuscata*) on Koshima Islet. *Primates*, 30: 17-25.

Imanishi K. (1960). Social organization of subhuman primates in their natural habitat. *Current Anthropology*, 1(5-6): 393-407.

Isbell L.A. and Young, T.P. (2002). Ecological models of female social relationships in primates: similarities, disparities, and some directions for future clarity. *Behaviour*, 139: 177-202.

Isbell L.A., Cheney D.L. and Seyfarth R.M. (2003). Why vervet monkeys (*Cercopithecus aethiops*) live in multimale groups. In: Glenn M.E. and Cords M. (Eds.), *The Guenons, Diversity and Adaptation in African Monkeys*, pp. 173-187. Kluwer Academic, New York, U.S.A.

Iwamoto T. and Dunbar R.I.M. (1983). Thermoregulation, habitat quality, and the behavioural ecology of gelada baboons. *Journal of Animal Ecology*, 52: 357-366.

Janson C.H. and Chapman C.A. (1999). Resources and primate community structure. In: Fleagle J.G., Janson C. and Reed K.E. (Eds.), *Primate Communities*, pp. 237-267. Cambridge University Press, Cambridge, U.K.

Janson C.H. and van Schaik, C.P. (1988). Recognizing the many faces of primate food competition: methods. *Behaviour*, 105: 165-186.

Jerison H.J. (1973). *Evolution of the Brain and Intelligence*. Academic Press, New York, U.S.A.

Johnson D.D.P., Kays R., Blackwell P.G. and Macdonald D.W. (2002). Does the resource dispersion hypothesis explain group living? *Trends in Ecology and Evolution*, 17: 563-570.

Judge P.G. (2000). Coping with crowded conditions. In: Aureli F. and de Waal F.B.M. (Eds.), *Natural Conflict Resolution*, pp. 129-154. University of California Press, Berkeley, U.S.A.

Judge P.G. and de Waal F.B.M. (1993). Conflict avoidance among rhesus monkeys: coping with short-term crowding. *Animal Behaviour*, 46: 221-232.

Judge P.G. and de Waal F.B.M. (1997). Rhesus monkey behaviour under diverse population densities: coping with long-term crowding. *Animal Behaviour*, 54: 643-662.

Kawamura S. (1958). Matriarchal social ranks in the Minoo-B troop: a study of the rank system of Japanese monkeys. *Primates*, 8: 189-216.

Kappeler P.M. and van Schaik C.P. (1992). Methodological and evolutionary aspects of reconciliation among primates. *Ethology*, 92: 51-69.

Kappeler P.M. and van Schaik C.P. (2002). Evolution and primate social systems. *International Journal of Primatology*, 23: 707-740.

Kapsalis E. and Berman C.M. (1996). Models of affiliative relationships among free-ranging rhesus monkeys (*Macaca mulatta*). II. Testing predictions for three hypothesised organizing principles. *Behaviour*, 133: 1235-1263.

Keverne E.B., Martensz N.D. and Tuite B. (1989). Beta-endorphin concentrations in cerebrospinal fluid of monkeys are influenced by grooming relationships. *Psychoneuroendocrinology,* 14: 155-161.

Koenig A., Beise J., Chalise M.K. and Ganzhorn J.U. (1998). When females should contest for food – testing hypotheses about resource density, distribution, size, and quality with Hanuman langurs (*Presbytis entellus*). *Behavioral Ecology and Sociobiology*, 42: 225-237.

Kohda M. (1985). Allomothering behaviour of New and Old World monkeys. *Primates*, 26: 28-44.

Kokko H., Mackenzie A., Reynolds J.D., Lindström J. and Sutherland W.J. (1999). Measures of inequality are not equal. *American Naturalist*, 72: 358-382.

Koyama N. (1970). Changes in dominance rank and division of a wild Japanese monkey troop in Arashiyama. *Primates*, 11, 335-390.

Koyama N. (1991). Grooming relationships in the Arashiyama group of Japanese monkeys. In: Fedigan L.M. and Asquith P. J. (Eds), *The Monkeys of Arashiyama: 35 Years of Research in Japan and the West,* pp. 211-226. State University of New York Press, Albany, U.S.A.

Koyama N.F. (2001). The long-term effects of reconciliation in Japanese macaques *Macaca fuscata*. *Ethology*, 107: 975-987.

Koyama N.F. (2003). Matrilineal cohesion and social networks in *Macaca fuscata*. *International Journal of Primatology*, 24: 797-811.

Koyama N.F. and Dunbar R.I.M. (1996). Anticipation of conflict by chimpanzees. *Primates*, 37: 79-86.

Kudo H. and Dunbar R.I.M. (2001). Neocortex size and social network size in primates. *Animal Behaviour*, 62: 711-722.

Kummer H. (1978). On the value of social relationships to non-human primates: a heuristic scheme. *Social Science Information*, 17: 687-705.

Kurland J.A. (1977). Kin selection in the Japanese monkeys. *Contributions to Primatology,* 12: 1-145. Karger, Basel, Switzerland.

Kutsukake N. and Castles D.L. (2001). Reconciliation and variation in post-conflict stress in Japanese macaques (*Macaca fuscata fuscata*): testing the integrated hypothesis. *Animal Cognition*, 4: 259-268.

Kutsukake K. and Clutton-Brock T.H. (2006). Social functions of allogrooming in cooperatively breeding meerkats. *Animal Behaviour*, 72: 1059-1068.

Lancaster J.B. (1972). Play-mothering: the relations between juvenile females and young infants among free-ranging vervets. In: Poirier F.E. (Ed.), *Primate Socialization*, pp. 113-139. Random House, New York, U.S.A.

Lazaro-Perea C., Arruda M.F. and Snowdon C.T. (2004). Grooming as a reward? Social function of grooming between females in cooperatively breeding marmosets. *Animal Behaviour*, 67: 627-636.

Leinfelder I., de Vries H., Deleu R. and Nelissen M. (2001). Rank and grooming reciprocity among females in a mixed-sex group of captive hamadryas baboons. *American Journal of Primatology*, 55: 25-42.

Lindenfors P., Fröberg L. and Nunn C.L. (2003). Females drive primate social evolution. *Proceedings of the Royal Society of London, B Series*, 271: 101-103.

Linn G.S., Mase D., Lafrancois D., O'Keefe R.T. and Lifshitz K. (1995). Social and menstrual cycle phase influences on the behaviour of group-housed *Cebus apella*. *American Journal of Primatology*, 35: 41-57.

Ljungberg T., Westlund K. and Lindqvist Forsberg A.J. (1999). Conflict resolution in 5-year-old boys: does postconflict affiliative behavior have a reconciliatory role? *Animal Behaviour*, 58: 1007-1016

Lorenz K. (1966). *On aggression*. Methuen, London, U.K.

Maestripieri D. (1993). Vigilance costs of allogrooming in macaque mothers. *American Naturalist*, 141: 744-753.

Maestripieri D., Schino G., Aureli F. and Troisi A. (1992). A modest proposal: displacement activities as an indicator of emotions in primates. *Animal Behaviour*, 44: 967-979.

Majolo B., Ventura R. and Koyama N.F. (2005). Sex, rank and age differences in the Japanese macaque (*Macaca fuscata yakui*) participation in inter-group encounters. *Ethology*, 111: 455-468.

Majolo B. 2004. *Conflict management in wild Japanese macaques (Macaca fuscata yakui)*. Unpublished Ph.D thesis, Liverpool John Moores University, U.K.

Mann J., Connor R.C., Tyack P.L. and Whitehead H. (2000). *Cetacean Societies: Field Studies of Dolphins and Whales*. University of Chicago Press, Chicago, U.S.A.

Manson J.H., Rose L.M., Perry S. and Gros-Luis J. (1999). Dynamics of female-female relationships in wild *Cebus capucinus*: data from two Costa Rican sites. *International Journal of Primatology*, 20: 679-706.

Manson J.H., Navarrete C.D., Silk J.B. and Perry S. (2004). Time-matched grooming in female primates? New analyses from two species. *Animal Behaviour*, 67: 493-500.

Martel F.L., Nevison C.M., Rayment F.D.G. and Simpson M.J.A. (1994). The social grooming of captive female rhesus monkeys: effects of the births of their infants. *International Journal of Primatology*, 15: 555-572.

Martin P. and Bateson P.P. 1993. *Measuring Behaviour*. Cambridge University Press, Cambridge, U.K.

Maruhashi T. 1980. Feeding behavior and diet of the Japanese monkey (*Macaca fuscata yakui*) on Yakushima Island, Japan. *Primates*, 21: 141-160.

Maruhashi T. (1982). An ecological study of troop fission of Japanese monkeys (*Macaca fuscata yakui*) on Yakushima Island, Japan. *Primates*, 23: 317-337.

Maruhashi T., Saito C. and Agetsuma N. (1998). Home range structure and inter-group competition for land of Japanese macaques in evergreen and deciduous forests. *Primates*, 39(3): 291-301.

Matheson M.D. and Bernstein I.S. (2000). Grooming, social bonding, and agonistic aiding in rhesus monkeys. *American Journal of Primatology*, 51: 177-186.

Mathy J.W. and Isbell L.A. (2001). The relative importance of size of food and interfood distance in eliciting aggression in captive rhesus macaques (*Macaca mulatta*). *Folia Primatologica*, 72: 268-277.

Matsumura S. (1996). The evolution of "egalitarian" and "despotic" social systems among macaques. *Primates*, 40: 23-31.

Mayagoitia L, Santillan-Doherty A.M., Lopez-Vergara L. and Mondragon-Ceballos R. (1993). Affiliation tactics prior to a period of competition in captive groups of stumptail macaques. *Ethology, Ecology and Evolution*, 5: 435-446.

Mc Farland Symington M. (1988). Food competition and foraging party size in the black spider monkey (*Ateles paniscus chamek*). *Behaviour*, 105: 117-134.

Mehlman P.T. and Chapais B. (1988). Differential effects of kinship, dominance, and the mating season on female allogrooming in a captive group of *Macaca fuscata*. *Primates,* 29: 195-217.

Melnick D.J. and Pearl M.C. (1987). Cercopithecines in multimale groups: genetic diversity and population structure. In: Smuts B.B., Cheney D.L., Seyfarth R.M., Wrangham R.W. and Struhsaker T.T. (Eds.), *Primate Societies*, pp. 121-134. University of Chicago Press, Chicago, U.S.A.

Mooring M.S. (1995). The effect of tick challenge on grooming rate by impala. *Animal Behaviour*, 50: 377-392.

Mooring M.S. and Hart B.L. (1995). Costs of allogrooming in impala: distraction from vigilance. *Animal Behaviour*, 49: 1414-1416.

Mooring M.S. and Hart B.L. (1997). Reciprocal allogrooming in wild impala lambs. *Ethology* 103: 665-680.

Mooring M.S., McKenzie A.A. and Hart B.L. (1996). Role of sex and breeding status in grooming and total tick load of impala. *Behavioral Ecology and Sociobiology*, 39: 259-266.

Morland H.S. (1993). Seasonal behavioural variation in and its relationship to thermoregulation in ruffled lemurs (*Vericia variegata variegata*). In: Kappler P.M. and Ganzhorn J.U. (Eds.), *Lemur Social Systems and Their Ecological Basis*, pp.193-203. Plenum, New York, U.S.A.

Moser R., Cords M. and Kummer H. (1991). Social influences on grooming site preferences among captive long-tailed macaques. *International Journal of Primatology,* 12: 217-230. GR-1

Moss C. (1988). *Elephant Memories*. William Morrow, New York, U.S.A.

Muroyama Y. (1991). Mutual reciprocity of grooming in female Japanese macaques (*Macaca fuscata*). *Behaviour*, 119: 161-170.

Muroyama Y. (1994). Exchange of grooming for allomothering in female patas monkeys. *Behaviour*, 128: 103-119.

Muroyama Y. (2002). Decision making in social interactions by monkeys. In: Matsuzawa T. (Ed.), *Primate Origins of Human Cognition and Behavior*, pp.463-483. Springer.

Muroyama Y., Imae H. and Okuda K. (2000). Radio tracking of a male Japanese macaque emigrated from its group. *Primates*, 41: 351-356.

Nakagawa N. (1989). Feeding strategies of Japanese monkeys against deterioration of habitat quality. *Primates*, 30: 1-16.

Nakagawa N. (1990). Choice of food patches by Japanese monkeys (*Macaca fuscata*). *American Journal of Primatology*, 21: 17-29.

Nakagawa N. (1992). Distribution of affiliative behaviors among adult females within a group of wild patas monkeys in a non-mating, nonbirth season. *International Journal of Primatology*, 13: 73-96.

Nakagawa N. (1998). Ecological determinants of the behavior and social structure of Japanese monkeys: a synthesis. *Primates*, 39: 375-383.

Nakagawa N., Iwamoto T., Yokota N. and Soumah A.G. (1997). Inter-regional and inter-seasonal variations of food quality in Japanese macaques: with reference to the constraints of digestive volume and feeding time. In: Fa J.E.

and Lindburg D.G. (Eds.), *Evolution and Ecology of Macaque Societies*, pp. 207-234. Cambridge University Press, Cambridge, U.K.

Nakamichi M. and Shizawa Y. (2003). Distribution of grooming among adult females in a large, free-ranging group of Japanese macaques. *International Journal of Primatology*, 24: 607-625.

Nakamura M. (2000). Is human conversation more efficient than chimpanzee grooming? Comparison of clique sizes. *Human Nature*, 11: 281-297.

Nakamura M. (2003). "Gatherings" of social grooming among wild chimpanzees: implications for evolution of sociality. *Journal of Human Evolution*, 44: 59-71.

Nicolson N.A. (1987). Infants, mothers, and other females. In: Smuts B.B., Cheney D.L., Seyfarth R.M., Wrangham R.W. and Struhsaker T.T. (Eds.), *Primate Societies*, pp. 330-342. The University of Chicago Press, Chicago, U.S.A.

Noë R. (1990). A veto game played by baboons: a challenge to the Prisoner's Dilemma as a paradigm for reciprocity and cooperation. *Animal Behaviour*, 39: 78-90.

Noë R. (2001). Biological markets: partner choice as the driving force behind the evolution of mutualisms. In: Noë R., van Hooff J.A.R.A.M. and Hammerstein P. (Eds.), *Economics in Nature*, pp. 93-118. Cambridge University Press, Cambridge, U.K.

Noë R. and Hammerstein P. (1994). Biological markets: supply and demand determines the effect of partner choice in cooperation, mutualism, and mating. *Behavioral Ecology and Sociobiology*. 35: 1-11.

Noë R. and Hammerstein P. (1995). Biological markets. *Trends in Ecology and Evolution,* 10: 336-339.

Noë R., van Hooff J.A.R.A.M. and Hammerstein P. (2001). *Economics in Nature*. Cambridge University Press, Cambridge, U.K.

Noldus Information Technology (1998) *MatMan Reference Manual, Version 1.0.* Wageningen, The Netherlands.

Noma N. (1997). Annual fluctuations of sapfruits production and synchronisation within and inter species in a warm temperate forest of Yakushima Island. *Tropics*, 6: 441-449.

Norberg R.A. (1977). An ecological theory on foraging time and energetic, and choice of optimal food-searching method. *Journal of Animal Ecology*, 46: 511-529.

Nunn C.L. (1999). The number of males in primate social groups: a comparative test of the socioecological model. *Behavioral Ecology and Sociobiology*, 46:1-13.

Nunn C.L. and van Schaik C.P. (2000). Social evolution in primates: the relative roles of ecology and intersexual conflict. In: Kappeler P.M. (Ed.), *Primate Males*, pp. 288-319. Cambridge University Press, Cambridge, U.K.

Nunn C.L., Gittleman J.L. and Antonovics J. (2000). Promiscuity and the primate immune system. *Science*, 290: 1168-1170.

Oates J.F. (1987). Food distribution and foraging behavior. In: Smuts B.B., Cheney D.L., Seyfarth R.M., Wrangham R.W. and Struhsaker T.T. (Eds.), *Primate Societies*, pp. 197-209. The University of Chicago Press, Chicago U.S.A.

O'Brien T.G. (1993). Allogrooming behaviour among female wedge-capped capuchin monkeys. *Animal Behaviour*, 46: 499-510.

O'Keefe R., Lifshits K. and Linn G. (1983). Relationships among dominance, inter-animal spatial proximity and affiliative social behavior in stumptail macaques (*Macaca arctoides*). *Applied Animal Ethology*, 9: 331-339.

Oki J. and Maeda Y. (1973). Grooming as a regulator of behavior in Japanese macaques. In: Carpenter C. R. (Ed.), *Behavioral Regulators of Behavior in Primates,* pp.149-163. Bucknell University Press, Lewisburg, PA, U.S.A.

Ostner J. (2002). Social thermoregulation in redfronted lemurs (*Eulemur fulvus rufus*). *Folia Primatologica*, 73: 175-180.

Palombit R., Seyfarth R.M. and Cheney D.L. (1997). The adaptive value of "friendships" to female baboons: experimental and observational evidence. *Animal Behaviour*, 54: 599-614.

Palombit R., Cheney D.L. and Seyfarth R.M. (2001). Female-female competition for male "friends" in wild chacma baboons, *Papio cynocephalus ursinus*. *Animal Behaviour*, 61: 1159-1171.

Parr L.A., Matheson M.D., Bernstein I.S. and de Waal F.BM. (1997). Grooming down the hierarchy: allogrooming in captive brown capuchin monkeys, *Cebus apella*. *Animal Behaviour*, 54: 361-367.

Pavani S., Maestripieri D., Schino G., Turillazzi P.G. and Scucchi S. (1991). Factors influencing scratching behaviour in long-tailed macaques (*Macaca fascicularis*). *Folia Primatologica*, 57: 34-38.

Perry S. (1996). Female-female social relationships in wild white-faced capuchin monkeys, *Cebus capucinus*. *American Journal of Primatology*, 40: 167-182.

Petit O., Abegg C. and Thierry B. (1997). A comparative study of aggression and reconciliation in three cercopithecine monkeys (*Macaca fuscata*, *Macaca nigra*, *Papio papio*). *Behaviour*, 134: 415-432.

Pochron S.T. (2000). Sun avoidance in the yellow baboons (*Papio cynocephalus cynocephalus*) of Ruaha National Park, Tanzania. Variation with season, behaviour and weather. *International Journal of Biometeorology*, 44: 141-147.

Pruetz J.D. and Isbell L.A. (2000). Correlations of food distribution and patch size with agonistic interactions in female vervets (*Chlorocebus aethiops*) and patas monkeys (*Erythrocebus patas*) living in simple habitats. *Behavioral Ecology and Sociobiology*, 49: 38-47.

Purvis A. (1995). A composite estimate of primate phylogeny. *Philosophical Transactions of the Royal Society of London, B Series*, 348: 405-421.

Pusey A.E. and Packer C. (1997). The ecology of relationships. In: Krebs J.R. and Davies N.B. (Eds.), *Behavioural Ecology: an Evolutionary Approach*, pp. 254-283. Blackwell Science, Oxford, U.K.

Pyke G.H., Pulliam H.R. and Charnov E.L. (1977). Optimal foraging: a selective review of theory and tests. *The Quarterly Review of Biology*, 52: 137- 154.

Rajagopalan P.K. and Anderson C.R. (1971). Further studies on ticks of wild monkeys of Kyasanur forest disease area, Shimoga district. *Indian Journal of Medical Research*, 59: 847-860.

Ridley M. (1996). *Evolution*. Blackwell Science, Cambridge.

Roberts G. and Sherratt T.N. (1998). Development of cooperative relationships through increasing investment. *Nature*, 394: 175-179.

Ron T., Henzi S.P. and Motro U. (1994). A new model of fission in primate troops. *Animal Behaviour*, 47: 223-226.

Rosenblum L.A., Kaufman I.C. and Stynes A.J. (1966). Some characteristics of adult social and autogrooming patterns in two species of macaque. *Folia Primatologica*, 4: 438-451.

Rowell T.E., Wilson C. and Cords M. (1991). Reciprocity and partner preference in grooming female blue monkeys. *International Journal of Primatology*, 12: 319-336.

Ruxton G.D. and Glasbey C.A. (1995). Energetics of group foraging: analysis of a random-walk model. *Journal of Mathematics Applied to Medicine and Biology*, 12:71-81.

Sade D.S. (1972). Sociometrix of *Macaca mulatta* I. Linkages and cliques in grooming matrices. *Folia Primatologica*, 18: 196-223.

Saito C. (1996). Dominance and feeding success in female Japanese macaques, *Macaca fuscata*: effects of food patch size and inter-patch distance. *Animal Behaviour*, 51: 967-980.

Saito C., Sato S., Suzuki S., Sugiura H., Agetsuma N., Takahata Y., Sasaki C., Takahashi H., Tanaka T. and Yamagiwa J. (1998). Aggressive intergroup encounters in two populations of Japanese macaques (*Macaca fuscata*). *Primates,* 39: 303-312.

Sambrook T.D., Whiten A. and Strum S.C. (1995). Priority of access and grooming patterns of females in a large and a small group of olive baboons. *Animal Behaviour*, 50: 1667-1682.

Saunders C.D. and Hausfater G. (1988). The functional significance of baboon grooming behavior. *Annals of the New York Academy of Sciences*, 525: 430-432.

Schino G. (2001). Grooming competition and social rank among female primates: a meta-analysis. *Animal Behaviour*, 62: 265-271.

Schino G. and Troisi A. (1990). Behavioral thermoregulation in long-tailed macaques: effect on social preferences. *Physiology and Behavior*, 47: 1125-1128.

Schino G and Troisi A. (1998). Mother-infant conflict over behavioral thermoregulation in Japanese macaques. *Behavioral Ecology and Sociobiology*, 43: 81-86.

Schino G., Scucchi S., Maestripieri D. and Turillazzi P.G. (1988). Allogrooming as a tension reduction mechanism: a behavioral approach. *American Journal of Primatology*, 16: 43-50.

Schino G., Perretta G., Taglioni A.M., Monaco V. and Troisi A. (1996). Primate displacement activities as an ethopharmacological model of anxiety. *Anxiety*, 2: 186-191.

Schino G., Rosati L. and Aureli F. (1998). Intragroup variation in conciliatory tendencies in captive Japanese macaques. *Behaviour*, 135: 897-912.

Schino G., Ventura R. and Troisi A. (2003). Grooming among female Japanese macaques: distinguishing between reciprocation and interchange. *Behavioral Ecology*, 14: 887-891.

Schino G., Ventura R. and Troisi A. (2005). Grooming and aggression in captive Japanese macaques. *Primates*, 46: 207–209.

Seyfarth R.M. (1976). Social relationships among adult female baboons. *Animal Behaviour* 24: 917-938.

Seyfarth R.M. (1977). A model of social grooming among adult female monkeys. *Journal of Theoretical Biology*, 65: 671-698.

Seyfarth R.M. (1980). The distribution of grooming and related behaviors among adult female vervet monkeys. *Animal Behaviour*, 28: 798-813.

Seyfarth R.M. and Cheney D.L. (1984). Grooming, alliances, and reciprocal altruism in vervet monkeys. *Nature*, 308: 541-543.

Seyfarth R.M. and Cheney D.L. (1988). Empirical tests of reciprocity theory: problems in assessment. *Ethology and Sociobiology*, 9:181-188.

Shannon C.E. and Wiener W. (1949). *The Mathematical Theory of Communication*. University of Illinois Press, Urbana, U.S.A.

Sherratt T.N. and Roberts G. (2002). The stability of cooperation involving variable investement. *Journal of Theoretical Biology*, 215: 47-56.

Siegel N. and Castellan J.Jr. (1988). *Nonparametric Statistics for the Behavioral Sciences*. Mc Graw-Hill, New York, U.S.A.

Silk J.B. (1982). Altruism among female *Macaca radiata*: explanation and analysis of patterns of grooming and coalition formation. *Behaviour*, 79: 162-188.

Silk J.B., Samuels A. and Rodman P.S. (1981). The influence of kinship, rank, and sex on affiliation and aggression between adult female and immature bonnet macaques (*Macaca radiata*). *Behaviour*, 79: 111-131.

Silk J.B., Seyfarth R.M. and Cheney D.L. (1999). The structure of social relationships among female savanna baboons in Moremi reserve, Botswana. *Behaviour*, 136: 679-703.

Soltis J., Thomsen R., Matsubayashi K. and Takenaka O. (2000). Infanticide by resident males and female counter-strategies in wild Japanese macaques (*Macaca fuscata yakui*). *Behavioral Ecology and Sociobiology*, 48: 195-202.

Soltis J., Thomsen R. and Takenaka O. (2001). The interaction of male and female reproductive strategies and paternity in wild Japanese macaques, *Macaca fuscata. Animal Behaviour*, 62: 485-494.

Sparks J. (1967). Allogrooming in Primates: a review. In: Morris D. (Ed.), *Primate Ethology*, pp.148-175. Wiedenfeld and Nicholson, London, U.K.

Sprague D.S. (1991). Mating by nontroop males among the Japanese macaques of Yakushima Island. *Folia Primatologica*, 57: 156-158.

Sprague D.S. (1992). Life history and male intertroop mobility among Japanese macaques (*Macaca fuscata*). *International Journal of Primatology*, 13: 437-454.

Sprague D.S. (1998). Age, dominance rank, natal status, and tenure among male macaques. *American Journal of Physical Anthropology*, 105: 511-521.

Sprague D.S., Suzuki S., Takahashi H. and Sato S. (1998). Male life history in natural populations of Japanese macaques: migration, dominance rank, and troop participation of males in two habitats. *Primates,* 39: 351-363.

Stammbach E. (1978). On social differentiation in groups of captive female hamadryas baboons. *Behaviour*, 67: 322-338.

Stammbach E. and Kummer H. (1982). Individual contributions to a dyadic interaction: an analysis of baboon grooming. *Animal Behaviour*, 30: 964-971.

Steenbeek R. and van Schaik C.P. (2001). Competition and group size in Thomas's langurs (*Presbytis thomasi*): the folivore paradox revisited. *Behavioral Ecology and Sociobiology*, 49: 100-110.

Stelzner J.K. (1988). Thermal effects on movement patterns of yellow baboons. *Primates*, 29: 91-105.

Stephens D.W. and Krebs J.R. 1986. *Foraging Theory*. Princeton University Press, Princeton, U.S.A.

Sterck E.H.M, Watts D.P. and van Schaik C.P. (1997). The evolution of female social relationships in nonhuman primates. *Behavioral Ecology and Sociobiology*, 41: 291-309.

Stopka P. and Graciasová R. (2001). Conditional allogrooming in the herb-field mouse. *Behavioral Ecology*, 12: 584-589.

Stopka P. and Macdonald D.W. (1999). The market effect in the wood mouse, *Apodemus sylvaticus*: selling information on reproductive status. *Ethology*, 105: 969-982.

Suchi S. and Rothe H. (1999). The influence of abiotic factors on the onset and cessation of activity of semi-free *Callithrix jacchus*. *American Journal of Primatology*, 47: 241-253.

Sugiura H., Saito C., Sato S., Agetsuma N., Takahashi H., Tanaka T., Furuichi T. and Takahata Y. (2000). Variation in intergroup encounters in two populations of Japanese macaques. *International Journal of Primatology*, 21: 519-535.

Sugiura H., Agetsuma N. and Suzuki S. (2002). Troop extinction and female fusion in wild Japanese macaques in Yakushima. *International Journal of Primatology*, 23: 69-84.

Suomi S.J. (1982). Abnormal behaviour in primate models of psychopathology. In: Fobes J. and King J. (Eds.), *Primate Behavior*, pp. 78-101. Academic Press, New York, U.S.A.

Takahashi H. (2002). Changes of dominance rank, age, and tenure of wild Japanese macaque males in the Kinkazan A troop during seven years. *Primates*, 43: 133-138.

Takahashi H. and Furuichi T. (1998). Comparative study of grooming relationships among wild Japanese macaques in Kinkazan A troop and Yakushima M troop. *Primates,* 39: 365-374.

Takahata Y., Suzuki S., Okayasu N. and Hill D. (1994). Troop extinction and fusion in wild Japanese macaques of Yakushima Island, Japan. *American Journal of Primatology*, 33: 317-322.

Tanaka I. and Takefushi H. (1993). Elimination of external parasites (lice) is the primary function of grooming in free-ranging Japanese macaques. *Anthropological Science*, 101: 187-193.

Tardif S.D. (1997). The bioenergetics of parental behaviour and the evolution of alloparental care in marmosets and tamarins. In: Solomen N.G. and French J.A. (Eds.), *Cooperative Breeding in Mammals*, pp. 11-33. Cambridge University Press, Cambridge, U.K.

Tattersall I. (1998). *Il Cammino dell'Uomo*. Garzanti, Turin, Italy.

Terry R.L. (1970). Primate grooming as a tension reduction mechanism. *Journal of Psychology*, 76: 129-136.

Thierry B. (2000). Covariation of conflict management patterns across macaque species. In: Aureli F. and de Waal F.B.M. (Eds.), *Natural Conflict Resolution*, pp. 106-128. University of California Press, Berkeley, CA, U.S.A.

Thierry B. (2004). Social epigenesis. In: Thierry B., Singh M. and Kaumanns W. (Eds.), *Macaque Societies*, pp. 267-290. Cambridge University of California Press, Cambridge, U.K.

Thierry B. Singh M. and Kaumanns W. (2004). *Macaque Societies*. Cambridge University of California Press, Cambridge, U.K.

Tomasello M. and Call J. (1997). *Primate Cognition*. Oxford University Press, New York, U.S.A.

Trivers R.L. (1971). The evolution of reciprocal altruism. *Quarterly Review of Biology*, 46: 35-57.

Trivers R.L. (1972). Parental investment and sexual selection. In: Campbell, P. (Ed.), *Sexual Selection and the Descent of Man*, pp. 136-179. Aldine, Chicago, U.S.A.

Trivers R.L. (1985). *Social Evolution*. Pearson Benjamin Cummings, U.S.A.

Troisi A., D'Amato F.R., Fuccillo R. and Scucchi S. (1982). Diurnal pattern of allogrooming in a group of Japanese macaques (*Macaca fuscata fuscata*). *Monitore Zooloologico Italiano*, 16: 149-160.

Troisi A. and Schino G. (1986). Diurnal and climatic influences on allogrooming behaviour in a captive group of Java monkeys. *Animal Behaviour*, 34: 1420-1426.

Troisi A. and Schino G. (1987). Environmental and social influences on autogrooming behaviour in a captive group of Java monkeys. *Behaviour*, 100: 292-303.

Troisi A., Schino G. and Aureli F. (1989). Allogrooming and interindividual proximity in two species of macaques (*Macaca fascicularis* and *Macaca nemestrina*). *Behaviour,* 111: 196-207.

van Hooff J.A.R.A.M. (2001). Conflict, reconciliation and negotitiation in non-human primates: the value of long-term relationships. In: Noë R., van Hooff J.A.R.A.M. and Hammerstein P. (Eds.), *Economics in Nature*, pp. 67-90. Cambridge University Press, Cambridge, U.K.

van Hooff J.A.R.A.M. and van Schaik C.P. (1992). Co-operation in competition: the ecology of primate bonds. In: Harcourt A.H. and de Waal F.B.M. (Eds.), *Coalition and Alliances in Humans and Other Animals*, pp. 357-390. Oxford University Press, Oxford, U.K.

van Schaik C.P. (1983). Why are diurnal primates living in groups? *Behaviour*, 87: 120-143.

van Schaik C.P. (1989). The ecology of social relatioships amongst female primates. In: Standen V. and Foley R.A. (Eds.), *Comparative Socioecology: the Behavioral Ecology of Humans and Other Mammals*, pp. 195-218. Blackwell, Oxford, U.K.

van Schaik C.P. (1996). Social evolution in primates: the role of ecological factors and male behaviour. *Proceedings of the British Academy*, 88: 9-31.

van Schaik C.P. and Deaner R.O. (2003). Life history and cognitive evolution in primates. In: de Waal F.B.M. and Tyack P.L. (Eds.), *Animal Social Complexity*, pp. 5-25. Harward University Press, Cambridge, MA, U.S.A.

van Schaik C.P. and Janson C.H. (2000). *Infanticide by Males and its Implications*. Cambridge University Press, Cambridge, U.K.

van Schaik C.P. and Pradhan G.R. (2003). A model of tool-use traditions in primates: implications for the coevolution of culture and cognition. *Journal of Human Evolution*, 44: 645-664.

van Schaik C.P. and van Noordwijk M.A. (1988). Scramble and contest in feeding competition among female long-tailed macaques (*Macaca fascicularis*). *Behaviour*, 105: 77-98.

van Schaik C.P., van Noordwijk M.A. and Nunn C.L. (1999). Sex and social evolution in primates. In: Lee P.C. (Ed.), *Comparative Primate Socioecology*, pp. 204-240. Cambridge University Press, Cambridge, U.K.

van Schaik C.P., van Noordwijk M.A., de Boer R.J. & den Tonkelaar I. (1983). The effect of group size on time budgets and social behaviour in wild long-tailed macaques (*Macaca fascicularis*). *Behavioural Ecology and Sociobiology*, 13: 173-181.

Veherecamp S. (1983). A model for the evolution of despotic versus egalitarian societies. *Animal Behaviour*, 31: 667-682.

Vervaecke H., de Vries H. and van Elsacker L. (2000). The pivotal role of rank in grooming and support behavior in a captive group of bonobos (*Pan paniscus*). *Behaviour*, 137: 1463-1485.

Watanabe K. (1979). Alliance formation in a free-ranging troop of Japanese macaques. *Primates*, 20: 459-574.

Watts D.P. (2000). Grooming between male chimpanzees at Ngogo, Kibale National Park. I. Partner number and diversity and grooming reciprocity. *International Journal of Primatology*, 21: 189-210.

White F.J. and Wrangham R.W. (1988). Feeding competition and patch size in the chimpanzee species *Pan paniscus* and *Pan troglodytes*. *Behaviour*, 105: 148-163.

Whitten P.L. (1988). Effects of patch size quality and feeding subgroup size on feeding success in vervet monkeys (*Cercopithecus aethiops*). *Behaviour*, 105: 35-52.

Wilson E.O. and Bossert W.H. (1971). *A Primer in Population Biology*. Sinauer Associates, Massachusetts, U.S.A.

Wrangham R.W. (1980). An ecological model of female-bonded primate groups. *Behaviour*, 75: 262-300.

Yamagiwa J. and Hill D.A. (1998). Intraspecific variation in the social organisation of Japanese macaques: past and present scope of field studies in natural habitats. *Primates*, 39: 257-274.

Yamagiwa J., Izawa K. and Maruhashi T. (1998). Long-term studies on wild Japanese macaques in natural habitats at Kinkazan and Yakushima: preface. *Primates*, 39: 255-256.

Yoshimi I. and Takasaki H. (2003). Long distance mobility of male Japanese macaques evidenced by mitochondrial DNA. *Primates*, 44: 71-74.

Zamma K. (2002). Grooming site preferences determined by lice infection among Japanese macaques in Arashiyama. *Primates*, 43: 41-49.

Zuckerman S. (1932). *The Social Life of Monkeys and Apes*. Kegan and Co., London, U.K.

APPENDIX A

Copy of the papers published using the data collected for this thesis.

The two published articles cited below (pp. 196-213) have been removed from the e-thesis due to copyright restrictions:

Ventura R., Majolo B., Koyama N.F., Hardie S. & Schino G. (2006) Reciprocation and interchange in wild Japanese macaques: Grooming, cofeeding and agonistic support. American Journal o f Primatology, 68: 1138-1149.

Ventura R., Majolo B., Schino G. & Hardie S. (2005). Differential effects of ambient temperature and humidity on allogrooming, self-grooming, and scratching in wild Japanese macaques. American Journal o f Physical Anthropology, 126: 453-457.

APPENDIX B

List of the main matrices used in this Thesis.

Appendix B.1: Matrix containing the amount of grooming reciprocated (% of observation time) among females in Nina A group (*close-kin females).

Monkey	Sya	Shi	Han	Ram	Hot	Htu	Yam	Yri
Sya		0.34	0.66	0.24	0.30	0.03	0.26	0.08
Shi	0.88		2.85	1.05	0.10	0	0.22	0.07
Han	0.73	2.62		0.21	0.12	0.04	0.09	0
Ram	0.50	1.09	0.74		2.83	1.15	0.72	0
Hot	0.40	0.05	0.12	2.80		3.13*	0.11	0
Htu	0.09	0	0.15	1.13	4.00*		0	0.23
Yam	0.25	0.19	0.25	0.47	0.09	0		3.23*
Yri	0.05	0.11	0.02	0	0	0.11	3.72*	

Appendix B.2: Matrix containing the amount of non-reciprocated grooming (% of observation time) among females in Nina A group (*close-kin females).

Monkey	Sya	Shi	Han	Ram	Hot	Htu	Yam	Yri
Sya		0.03	0.73	0.03	0.01	0	0.11	0.04
Shi	0.79		1.22	0.33	0.04	0	0.16	0
Han	0.37	0.78		0.07	0	0.04	0	0
Ram	0.23	0.40	0.72		0.22	0.24	0.23	0
Hot	0.54	0.15	0.37	0.44		1.34*	0.45	0.01
Htu	0.03	0.08	0.04	0.38	0.57*		0.06	0.05
Yam	0.54	0.54	0.31	0.21	0.04	0.05		0.70*
Yri	0.19	0.31	0.13	0.05	0	0	1.19*	

Appendix B.3: Matrices containing the difference between grooming given and received (proportion of observation time) among females in Nina A (a) and Kw (b) group (*close-kin females in Nina A group).

(a)

Monkey	Sya	Shi	Han	Ram	Hot	Htu	Yam	Yri
Sya		-0.05	0.01	-0.01	-0.03	0	-0.03	-0.01
Shi	0.05		0.03	-0.03	-0.01	0	-0.02	-0.01
Han	-0.01	-0.03		-0.06	-0.02	-0.01	-0.05	-0.01
Ram	0.01	0.03	0.06		0	-0.01	0.03	0.01
Hot	0.03	0.01	0.02	0		0.03*	0.01	0
Htu	0	0	0.01	0.01	-0.03*		0	0.01
Yam	0.03	0.02	0.05	-0.03	-0.01	0		0.45*
Yri	0.01	0.01	0.01	-0.01	0	-0.01	-0.45*	

(b)

Monkey	Ani	Ann	Bla	Chi	Cho	Dor	Eli	Elz	Fum	Hnn	Jun	Kik	Liv	Miy	Nob	Oli	Raf	Sar	Zaz	Zin
Ani		-0.0265	0.0240	0	0	0	-0.0148	-0.0024	-0.0679	0	0.0150	0.0045	0.0001	0	0	0.0093	0	0	0	0
Ann	-0.0265		0	0	0	0	0	0	-0.0025	0	0	0.1024	0.0015	0	0	0.0676	0	0	-0.0009	0
Bla	0.0240	0		0	0.0065	0.0122	-0	0	0.0226	0.0091	0	0	0	0.0099	0.0071	0.0006	0.0386	0	0	-0.0056
Chi	0	0	0		0.0010	0	0	0.0002	0	0	0	0	0	0	0.0032	0	0	0.0047	0.0011	0.1305
Cho	0	0	-0.0065	-0.0010		-0.0088	-0.0316	-0.0315	0	0	-0.0075	0	-0.0006	0	-0.0154	0	0	-0.0002	-0.0057	-0.0055
Dor	0	0	-0.0122	0	-0.0088		-0.0026	0	-0.0034	-0.0026	-0.0168	-0.0003	-0.0117	-0.0016	-0.0300	0	-0.0046	-0.0018	-0.0148	-0.0381
Eli	0.0148	0	0	0	0.0316	0.0026		0.0171	0	0	0	0.0012	0.0001	0	0.0007	0.0056	0.0020	0.0019	0.0005	0
Elz	0.0024	0	0	0.0002	0.0315	0	0.0171		0	0	0.0009	0.0012	0	0	0	0	0	0	0	0
Fum	0.0679	0.0025	0.0226	0	0	0.0034	0	0		0	0	0.0300	0	0	0	0	0	0	0	0
Hnn	0	0	-0.0091	0	0	0.0026	0	0	0		0.0199	0	0	0.0097	0	0	0.0080	0	0	0
Jun	-0.0150	0	0	0	0.0075	0.0168	0	0.0009	0	0.0199		0	0.0475	0	0.0079	0	0.0113	0.0180	0.0187	0.0060
Kik	-0.0045	-0.1024	0	0	0	0.0003	0.0012	0.0012	0.0300	0	0		0	0	0.0034	0.0127	0	0	0	0
Liv	-0.0001	0.0015	0	0	0.0006	0.0117	0.0001	0	0	0	0.0475	0		0	0.0015	0.0051	0.0013	0.0002	0.0070	0.0152
Miy	0	0	-0.0099	0	0	0.0016	0	0	0	0.0097	0	0	0		0	0	0	0	0	0
Nob	0	0	0.0071	0.0032	0.0154	0.0300	0.0007	0	0	0	0.0079	0.0034	0.0015	0		0.0028	0.0186	0.0034	0.0052	0.0049
Oli	-0.0093	-0.0676	-0.0006	0	0	0	0.0056	0	0	0	0	0.0127	0.0051	0	0.0028		0	0	0	0

| | | |

Appendix B.4: Matrices containing the signed rank distance between groomer and groomee in Nina A (a) and Kw (b) group (*close-kin females in Nina A group).

(a)

Monkey	Sya	Shi	Han	Ram	Hot	Htu	Yam	Yri
Sya		-1	-2	-5	-6	-7	-3	-4
Shi	1		-1	-4	-5	-6	-2	-3
Han	2	1		-3	-4	-5	-1	-2
Ram	5	4	3		-1	-2	2	1
Hot	6	5	4	1		-1*	3	2
Htu	7	6	5	2	1*		4	3
Yam	3	2	1	-2	-3	-4		-1*
Yri	4	3	2	-1	-2	-3	1*	

(b)

Monkey	Ani	Ann	Bla	Chi	Cho	Dor	Eli	Elz	Fum	Hnn	Jun	Kik	Liv	Miy	Nob	Oli	Raf	Sar	Zaz	Zin
Ani		-2	5	2	-4	9	-6	-7	5	5	11	-1	10	5	5	-4	-4	1	8	12
Ann	2		7	4	-2	11	-4	-5	7	7	13	1	12	7	7	-2	-2	3	10	14
Bla	-5	-7		-3	-9	4	-11	-12	0	0	6	-6	5	0	0	-9	-9	-4	3	7
Chi	-2	-4	3		-6	7	-8	-9	3	3	9	-3	8	3	3	-6	-6	-1	6	10
Cho	4	2	9	6		13	-2	-3	9	9	15	3	14	9	9	0	0	5	12	16
Dor	-9	-11	-4	-7	-13		-15	-16	-4	-4	2	-10	1	-4	-4	-13	-13	-8	1	3
Eli	6	4	11	8	2	15		-1	11	11	17	5	16	11	11	2	2	7	14	18
Elz	7	5	12	9	3	16	1		12	12	18	6	17	12	12	3	3	8	15	19
Fum	-5	-7	0	-3	-9	4	-11	-12		0	6	-6	5	0	0	-9	-9	-4	3	7
Hnn	-5	-7	0	-3	-9	4	-11	-12	0		6	-6	5	0	0	-9	-9	-4	3	7
Jun	-11	-13	-6	-9	-15	-2	-17	-18	-6	-6		-12	-1	-6	-6	-15	-15	-10	-3	1
Kik	1	-1	6	3	-3	10	-5	-6	6	6	12		11	6	6	-3	-3	2	9	13
Liv	-10	-12	-5	-8	-14	-1	-16	-17	-5	-5	1	-11		-5	-5	-14	-14	-9	-2	2
Miy	-5	-7	0	-3	-9	4	-11	-12	0	0	6	-6	5		0	-9	-9	-4	3	7
Nob	-5	-7	0	-3	-9	4	-11	-12	0	0	6	-6	5	0		-9	-9	-4	3	7
Oli	4	2	9	6	0	13	-2	-3	9	9	15	3	14	9	9		0	5	12	16
Raf	4	2	9	6	0	13	-2	-3	9	9	15	3	14	9	9	0		5	12	16
Sar	-1	-3	4	1	-5	8	-7	-8	4	4	10	-2	9	4	4	-5	-5		7	11
Zaz	-8	-10	-3	-6	-12	1	-14	-15	-3	-3	3	-9	2	-3	-3	-12	-12	-7		4
Zin	-12	-14	-7	-10	-16	-3	-18	-19	-7	-7	-1	-13	-2	-7	-7	-16	-16	-11	-4	

Appendix B.5: Matrix containing the amount of grooming given in the period February-April (% of observation time) among females in Nina A group (*close-kin females).

Monkey	Sya	Shi	Han	Ram	Hot	Htu	Yam	Yri
Sya		1.34	2.10	0.58	0.32	0	1.00	0.62
Shi	7.04		13.72	1.99	0.23	0	0.03	0
Han	1.83	6.05		2.35	0	0	0.15	0
Ram	3.93	8.63	7.69		3.83	6.68	4.36	0.15
Hot	4.35	1.29	0	2.72		7.58*	1.73	0
Htu	0	0.17	0	5.50	6.86*		0	0.60
Yam	2.76	1.98	3.85	2.09	1.26	0		8.05*
Yri	0.50	1.13	0.40	0.05	0	1.00	12.08	

Appendix B.6: Matrix containing the amount of grooming given in the period July-August (% of observation time) among females in Nina A group (*close-kin females).

Monkey	Sya	Shi	Han	Ram	Hot	Htu	Yam	Yri
Sya		0.03	1.35	0.46	1.04	0	1.06	0.50
Shi	0.67		4.25	1.26	2.25	0	1.24	0.80
Han	0.14	4.31		0.13	0.53	0.05	0.25	0.36
Ram	0.17	3.80	10.14		9.36	2.02	4.21	0
Hot	5.57	2.32	6.74	12.54		7.82*	3.87	1.57
Htu	0.85	0.55	1.19	2.62	4.25*		0	0.84
Yam	2.90	4.33	1.61	1.09	1.52	0		10.60*
Yri	3.44	1.71	1.96	0	0	0	10.11*	

Appendix B.7: Matrix containing the difference between grooming given and received in the period February-April (proportion of observation time) among females in Nina A group (*close-kin females).

Monkey	Sya	Shi	Han	Ram	Hot	Htu	Yam	Yri
Sya		-0.0570	0.0027	-0.0335	-0.0403	0	-0.0176	0.0012
Shi	0.0570		0.0767	-0.0664	-0.0107	-0.0018	-0.0195	-0.0113
Han	-0.0027	-0.0767		-0.0535	0	0	-0.0370	-0.0041
Ram	0.0335	0.0664	0.0535		0.0112	0.0117	0.0227	0.0011
Hot	0.0403	0.0107	0	-0.0112		0.0071*	0.0047	0
Htu	0	0.0018	0	-0.0117	-0.0071*		0	-0.0041
Yam	0.0176	0.0195	0.0370	-0.0227	-0.0047	0		-0.0403*
Yri	-0.0012	0.0113	0.0041	-0.0011	0	0.0041	0.0403*	

Appendix B.8: Matrix containing the difference between grooming given and received in the period July-August (proportion of observation time) among females in Nina A group (*close-kin females).

Monkey	Sya	Shi	Han	Ram	Hot	Htu	Yam	Yri
Sya		-0.006	0.012	0.002	-0.045	-0.008	-0.018	-0.029
Shi	0.006		-0.000	-0.025	0	-0.005	-0.030	-0.009
Han	-0.012	0		-0.100	-0.062	-0.011	-0.013	-0.015
Ram	-0.002	0.025	0.100		-0.031	-0.005	0.031	0
Hot	0.045	0	0.062	0.031		0.035*	0.023	0.015
Htu	0.008	0.005	0.011	0.005	-0.035*		0	0.008
Yam	0.018	0.030	0.013	-0.031	-0.023	0		0.004*
Yri	0.029	0.009	0.015	0	-0.015	-0.008	-0.004*	

Appendix B.9: Matrix containing the amount of grooming given (% of observation time) among females in Kw group.

Monkey	Ani	Ann	Bla	Chi	Cho	Dor	Eli	Elz	Fum	Hnn	Jun	Kik	Liv	Miy	Nob	Oli	Raf	Sar	Zaz	Zin
Ani		0.03	2.40	0	0	0	0	0	5.02	0	1.70	0.45	0.12	0	0	1.24	0	0	0	0
Ann	2.67		0	0	0	0	0	0	5.23	0	0	12.60	0	0	0	7.96	0	0	0	0
Bla	0	0		0	0.65	0.68	0	0	1.89	6.95	0	0	0	5.37	0.57	0.06	7.41	0	0	0.12
Chi	0	0	0		0.77	0	0	0	0	0	0	0	0	0	0.44	0	0	12.22	0	0
Cho	0	0	0	0.68		1.60	9.49	8.41	0	0	0.89	0	0.57	0	1.24	0	0	0	0	0.78
Dor	0	0	1.90	0	0.72		0.92	0	0	0.08	2.75	0.03	1.76	0.04	3.31	0	0.57	0.85	4.15	3.95
Eli	1.48	0	0	0	12.65	1.18		2.83	0	0	0	0.88	0	0	0.41	0.68	1.12	0	0.05	0
Elz	0.24	0	0	0.02	5.26	0	1.11		0	0	0.09	0	0	0	0	0	0	0	0	0
Fum	11.80	5.47	4.14	0	0	0.34	0	0		0	0	5.09	0	0	0	0	0	0	0	0
Hnn	0	0	6.04	0	0	0.35	0	0	0		2.05	0	0	10.44	0	0	2.35	0	0	0
Jun	0.20	0	0	0	0.14	1.06	0	0	0	0.06		0	10.54	0	0.05	0	0	0.31	1.80	2.33
Kik	0	2.36	0	0	0	0.07	1.00	0.12	2.09	0	0		0	0	0.74	3.49	0	0	0	0
Liv	0.11	0.15	0	0	0.51	0.60	0.01	0	0	0	5.78	0		0	0.39	0.51	0.07	1.18	1.26	2.55
Miy	0	0	4.38	0	0	0.20	0	0	0	9.47	0	0	0		0	0	0	0	0	0
Nob	0	0	1.28	0.76	2.78	6.32	0.34	0	0	0	0.84	0.40	0.24	0		0.62	5.19	3.24	3.72	0.08
Oli	0.30	1.19	0	0	0	0	0.12	0	0	0	0	2.23	0	0	0.35		0	0	0	0
Raf	0	0	11.27	0	0	1.03	1.32	0	0	3.15	1.13	0	0.20	0	3.33	0		0	0	0
Sar	0	0	0	11.75	0.02	1.02	0.19	0	0	0	2.11	0	1.17	0	3.58	0	0		1.18	0.64
Zaz	0	0.09	0	0.11	0.57	2.66	0	0	0	0	3.67	0	1.96	0	3.20	0	0	0.92		4.52
Zin	0	0	0.68	13.05	0.24	7.77	0	0	0	0	2.93	0	1.03	0	0.57	0	0	0	4.66	

Appendix B.10: Matrix containing the rank of female groomees in Kw group.

Monkey	Ani	Ann	Bla	Chi	Cho	Dor	Eli	Elz	Fum	Hnn	Jun	Kik	Liv	Miy	Nob	Oli	Raf	Sar	Zaz	Zin
Ani		15	8	11	17	4	19	20	8	8	2	14	3	8	8	17	17	12	5	1
Ann	13		8	11	17	4	19	20	8	8	2	14	3	8	8	17	17	12	5	1
Bla	13	15		11	17	4	19	20	8	8	2	14	3	8	8	17	17	12	5	1
Chi	13	15	8		17	4	19	20	8	8	2	14	3	8	8	17	17	12	5	1
Cho	13	15	8	11		4	19	20	8	8	2	14	3	8	8	17	17	12	5	1
Dor	13	15	8	11	17		19	20	8	8	2	14	3	8	8	17	17	12	5	1
Eli	13	15	8	11	17	4		20	8	8	2	14	3	8	8	17	17	12	5	1
Elz	13	15	8	11	17	4	19		8	8	2	14	3	8	8	17	17	12	5	1
Fum	13	15	8	11	17	4	19	20		8	2	14	3	8	8	17	17	12	5	1
Hnn	13	15	8	11	17	4	19	20	8		2	14	3	8	8	17	17	12	5	1
Jun	13	15	8	11	17	4	19	20	8	8		14	3	8	8	17	17	12	5	1
Kik	13	15	8	11	17	4	19	20	8	8	2		3	8	8	17	17	12	5	1
Liv	13	15	8	11	17	4	19	20	8	8	2	14		8	8	17	17	12	5	1
Miy	13	15	8	11	17	4	19	20	8	8	2	14	3		8	17	17	12	5	1
Nob	13	15	8	11	17	4	19	20	8	8	2	14	3	8		17	17	12	5	1
Oli	13	15	8	11	17	4	19	20	8	8	2	14	3	8	8		17	12	5	1
Raf	13	15	8	11	17	4	19	20	8	8	2	14	3	8	8	17		12	5	1
Sar	13	15	8	11	17	4	19	20	8	8	2	14	3	8	8	17	17		5	1
Zaz	13	15	8	11	17	4	19	20	8	8	2	14	3	8	8	17	17	12		0
Zin	13	15	8	11	17	4	19	20	8	8	2	14	3	8	8	17	17	12	5	

Appendix B.11: Matrices containing the frequency of grooming solicitations (events / hour) in Nina A (a) and Kw (b) group (*close-kin females in Nina A group).

(a)

Monkey	Sya	Shi	Han	Ram	Hot	Htu	Yam	Yri
Sya		0.98	0.41	0.35	0.33	0	0.19	0
Shi	0.33		1.18	0.70	0.13	0	0.07	0
Han	0.62	4.36		1.26	0	0	0.34	0
Ram	0.14	0.49	0.67		0.35	1.07	0.42	0
Hot	0.26	0.07	0	0.78		0.88*	0.13	0
Htu	0	0	0	1.14	2.77*		0	0.21
Yam	0.39	0.07	0.07	1.25	0.26	0		3.58*
Yri	0	0	0	0	0	0	1.62*	

(b)

Monkey	Ani	Ann	Bla	Chi	Cho	Dor	Eli	Elz	Fum	Hnn	Jun	Kik	Liv	Miy	Nob	Oli	Raf	Sar	Zaz	Zin
Ani		0.14	0	0	0	0	0	0	1.54	0.07	0.07	0	0	0	0	0	0	0	0	0
Ann	0.21		0	0	0	0	0	0	0.41	0	0	0.21	0	0	0	0.36	0	0	0	0
Bla	0	0		0	0	0.14	0	0	0.21	0.98	0.07	0	0	0.90	0.14	0	1.44	0	0	0.07
Chi	0	0	0		0	0	0	0	0	0	0	0	0	0	0.18	0	0	2.41	0	0
Cho	0	0	0.07	0		0.20	5.11	4.78	0	0	0	0	0.07	0	0.35	0	0	0	0	0.14
Dor	0.07	0	0.14	0	0.07		0	0	0	0	0.33	0	0.07	0	0.74	0	0.20	0.07	0.54	1.06
Eli	0	0	0	0	1.68	0		0.71	0	0	0	0.14	0	0	0.07	0	0.07	0.07	0	0
Elz	0	0	0	0	2.01	0	0.78		0	0	0	0	0	0	0	0	0	0	0	0
Fum	1.14	1.16	0	0	0	0	0	0		0	0	0.35	0	0	0	0	0	0	0	0
Hnn	0.07	0	0.68	0	0	0.07	0	0	0		0.07	0	0	2.56	0	0	0.60	0	0	0
Jun	0.20	0	0	0	0.14	0.13	0	0.14	0	0.15		0	0.27	0	0.07	0	0.07	0.14	0.27	0.20
Kik	0	2.63	0	0	0	0	0.07	0	0.41	0	0		0	0	0.07	0.50	0	0	0	0
Liv	0.07	0	0	0	0	0.13	0	0	0	0	0.93	0		0	0.07	0	0	0.14	0.07	0.13
Miy	0	0	0.30	0	0	0	0	0	0	1.70	0	0	0		0	0	0	0	0	0
Nob	0	0	0.21	0	0.14	0.34	0.14	0	0	0	0	0.07	0	0		0	1.21	0.49	0.98	0.07
Oli	0	1.64	0	0	0	0	0	0	0	0	0	1.23	0	0	0		0	0	0	0
Raf	0	0	0.72	0	0	0.07	0.29	0	0	0.15	0	0	0.07	0	0.43	0		0	0	0
Sar	0	0	0	3.40	0	0.27	0.21	0	0	0	0.07	0	0.07	0	0.49	0	0		0.14	0
Zaz	0	0	0	0	0.07	0.47	0	0	0	0	0.55	0	0	0	1.32	0	0	0.14		0.41
Zin	0	0	0	0	0.07	0.07	0	0	0	0	0.34	0	0.20	0	0.14	0	0	0	0.27	

Appendix B.12: Matrices containing the proportion of successful grooming solicitations (N of solicitations followed by grooming / total N of solicitations) in Nina A (a) and Kw (b) group (*close-kin females in Nina A group).

(a)

Monkey	Sya	Shi	Han	Ram	Hot	Htu	Yam	Yri
Sya		0.87	0.83	0.80	1.00	0	0.67	0
Shi	0.80		0.82	0.90	1.00	0	0	0
Han	0.78	0.71		0.82	0	0	1.00	0
Ram	1.00	0.86	0.89		1.00	0.87	0.67	0
Hot	1.00	1.00	0	1.00		0.92*	0.50	0
Htu	0	0	0	0.94	0.93*		0	1.00
Yam	0.50	1.00	1.00	0.89	0.50	0		0.92*
Yri	0	0	0	0	0	0	0.88*	

(b)

Monkey	Ani	Ann	Bla	Chi	Cho	Dor	Eli	Elz	Fum	Hnn	Jun	Kik	Liv	Miy	Nob	Oli	Raf	Sar	Zaz	Zin
Ani		1.00	0	0	0	0	0	0	0.78	0	1.00	0	0	0	0	0	0	0	0	0
Ann	0.67		0	0	0	0	0	0	0.83	0	0	0.67	0	0	0	0.80	0	0	0	0
Bla	0	0		0	0	1.00	0	0	0.67	0.85	0	0	0	0.50	0.50	0	0.65	0	0	1.00
Chi	0	0	0		0	0	0	0	0	0	0	0	0	0	0.50	0	0	0.85	0	0
Cho	0	0	1.00	0		1.00	0.33	0.87	0	0	0	0	1.00	0	0.80	0	0	0	0	1.00
Dor	0	0	1.00	0	1.00		0	0	0	0	0.80	0	1.00	0	0.73	0	0.67	1.00	0.63	0.88
Eli	0	0	0	0	0.92	0		0.70	0	0	0	0.50	0	0	1.00	0	1.00	1.00	0	0
Elz	0	0	0	0	0.41	0	0.64		0	0	0	0	0	0	0	0	0	0	0	0
Fum	1.00	0.94	0	0	0	0	0	0		0	0	1.00	0	0	0	0	0	0	0	0
Hnn	0	0	1.00	0	0	0	0	0	0		1.00	0	0	0.70	0	0	0.75	0	0	0
Jun	1.00	0	0	0	0.50	1.00	0	0.50	0	1.00		0	0.75	0	1.00	0	1.00	0.50	0.75	1.00
Kik	0	0.86	0	0	0	0	1.00	0	1.00	0	0		0	0	1.00	1.00	0	0	0	0
Liv	1.00	0	0	0	0	1.00	0	0	0	0	1.00	0		0	1.00	0	0	0.50	1.00	1.00
Miy	0	0	1.00	0	0	0	0	0	0	0.82	0	0	0		0	0	0	0	0	0
Nob	0	0	0.67	0	1.00	0.80	0	0	0	0	0	0	0	0		0	0.65	1.00	0.79	1.00
Oli	0	0.74	0	0	0	0	0	0	0	0	0	0.88	0	0	0		0	0	0	0
Raf	0	0	0.90	0	0	0	0.75	0	0	0.50	0	0	1.00	0	0.33	0		0	0	0
Sar	0	0	0	0.74	0	0.50	0	0	0	0	1.00	0	1.00	0	0.71	0	0		1.00	0
Zaz	0	0	0	0	3.00	0.57	0	0	0	0	0.63	0	0	0	0.58	0	0	1.00		1.00
Zin	0	0	0	0	1.00	1.00	0	0	0	0	0.80	0	1.00	0	0.50	0	0	0	0.75	

Appendix B.13: Matrices containing the frequency of aggression received (events / hour) by females in Nina A (a) and Kw (b) group (*close-kin females in Nina A group).

(a)

Monkey	Sya	Shi	Han	Ram	Hot	Htu	Yam	Yri
Sya		0	0	0.000005	0	0.000011	0.000046	0.000016
Shi	0		0.000005	0.000006	0.000005	0.000006	0.000005	0.000011
Han	0	0		0.000027	0.000043	0.000005	0.000031	0.000016
Ram	0	0	0		0.000016	0.000038	0	0
Hot	0	0	0	0		0.000033*	0	0
Htu	0	0	0	0	0*		0	0
Yam	0	0	0	0.000005	0.000011	0.000016		0.000058*
Yri	0	0	0	0.000005	0	0.000022	0*	

(b)

Monkey	Ani	Ann	Bla	Chi	Cho	Dor	Eli	Elz	Fum	Hnn	Jun	Kik	Liv	Miy	Nob	Oli	Raf	Sar	Zaz	Zin
Ani		0	0	0	0	0	0	0	0	0	0	0.0000 193	0	0	0	0	0	0	0	0
Ann	0		0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Bla	0	0		0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Chi	0	0	0		0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Cho	0	0	0	0		0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Dor	0	0.0000 188	0	0	0		0	0	0.0000 365	0	0	0.0000 190	0	0	0	0	0.0000 379	0.0000 188	0.0000 372	0
Eli	0	0	0	0	0	0		0	0	0	0	0	0	0	0	0	0	0	0	0
Elz	0	0	0	0	0	0	0		0	0	0	0	0	0	0	0	0	0	0	0
Fum	0.0000 557	0	0	0	0	0	0	0		0	0	0	0	0	0	0.0000 193	0	0	0	0
Hnn	0	0	0	0	0	0	0	0	0		0	0	0	0	0	0	0	0	0	0
Jun	0	0	0	0	0	0	0	0	0	0		0.0000 195	0.0000 370	0.0000 202	0	0	0	0	0	0
Kik	0	0	0	0	0	0	0	0	0	0	0		0	0	0	0.0000 200	0	0	0	0
Liv	0.0000 550	0	0.0000 403	0	0.0000 740	0.0000 181	0	0	0	0.0000 197	0	0		0	0	0	0	0.0000 188	0.0000 744	0
Miy	0	0	0	0	0	0	0	0	0	0	0	0	0		0	0	0	0	0	0

Nob												0.0000								
	0	0	0	0	0	0	0	0	0	0	0	198	0	0		0	0	0	0	0
Oli					0.0000															
	0	0	0	0	195	0	0	0	0	0	0	0	0	0	0		0	0	0	0
Raf	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0		0	0	0
Sar					0.0000															
	0	0	0	0	385	0	0	0	0	0	0	0	0	0	0	0	0		0	0
Zaz					0.0000												0.0000			
	0	0	0	0	191	0	0	0	0	0	0	0	0	0	0	0	195	0		0
Zin	0.0000		0.0000			0.0000					0.0000		0.0000	0.0000		0.0000			0.0000	
	750	0	403	0	0	185	0	0	0	0	189	0	185	201	0	195	0	0	571	

Appendix B.14: Matrices containing the number of times two females were seen foraging on the same food patch in Nina A (a) and Kw (b) group (*close-kin females in Nina A group).

(a)

Monkey	Sya	Shi	Han	Ram	Hot	Htu	Yam	Yri
Sya		44	51	22	34	18	40	24
Shi	44		34	24	34	11	24	12
Han	51	34		17	28	15	35	21
Ram	22	24	17		19	13	19	12
Hot	34	34	28	19		16*	29	15
Htu	18	11	15	13	16*		14	9
Yam	40	24	35	19	29	14		24*
Yri	24	12	21	12	15	9	24*	

(b)

Monkey	Ani	Ann	Bla	Chi	Cho	Dor	Eli	Elz	Fum	Hnn	Jun	Kik	Liv	Miy	Nob	Oli	Raf	Sar	Zaz	Zin
Ani		1	0	1	1	0	0	0	4	0	4	1	4	3	2	1	1	0	4	5
Ann	1		0	1	0	0	0	0	4	1	0	4	0	0	0	2	0	0	0	0
Bla	0	0		0	1	2	0	0	1	0	2	0	1	0	0	2	1	1	1	1
Chi	1	1	0		0	0	0	0	0	1	0	0	0	1	0	1	0	1	0	0
Cho	1	0	1	0		3	1	0	1	0	6	1	4	0	0	2	0	1	2	2
Dor	0	0	2	0	3		2	0	1	0	7	1	10	0	2	1	1	0	2	4
Eli	0	0	0	0	1	2		0	0	0	0	0	1	0	0	0	0	0	0	2
Elz	0	0	0	0	0	0	0		0	0	1	0	1	0	0	0	0	1	1	2
Fum	4	4	1	0	1	1	0	0		0	0	2	1	1	0	6	0	0	1	2
Hnn	0	1	0	1	0	0	0	0	0		0	0	0	3	0	1	0	0	0	0
Jun	4	0	2	0	6	7	0	1	0	0		0	10	0	2	2	2	0	5	9
Kik	1	4	0	0	1	1	0	0	2	0	0		0	0	1	1	1	0	1	0
Liv	4	0	1	0	4	10	1	1	1	0	10	0		1	2	2	2	1	5	8
Miy	3	0	0	1	0	0	0	0	1	3	0	0	1		1	1	0	1	2	1
Nob	2	0	0	0	0	2	0	0	0	0	2	1	2	1		0	0	0	3	2
Oli	1	2	2	1	2	1	0	0	6	1	2	1	2	1	0		0	1	3	2
Raf	1	0	1	0	0	1	0	0	0	0	2	1	2	0	0	0		1	1	0
Sar	0	0	1	1	1	0	0	1	0	0	0	0	1	1	0	1	1		4	2
Zaz	4	0	1	0	2	2	0	1	1	0	5	1	5	2	3	3	1	4		7
Zin	5	0	1	0	2	4	2	2	2	0	9	0	8	1	2	2	0	2	7	

Appendix B.15: Matrices containing the amount of female co-feeding (% of observation time spent in proximity, i.e. ≤ 1 meter, during foraging) in Nina A (a) and Kw (b) group (*close-kin females in Nina A group).

(a)

Monkey	Sya	Shi	Han	Ram	Hot	Htu	Yam	Yri
Sya		0.619	0.589	0	0.030	0	0.020	0.005
Shi	1.520		0.139	0.336	0	0	0.113	0.031
Han	0.406	0.447		0.053	0.038	0	0.800	0.344
Ram	0.442	0.260	0.021		0.004	0.107	0.012	0
Hot	0.263	0.029	0.315	0		0.067*	0.174	0.012
Htu	0.064	0	0.031	0.012	0.182*		0.052	0.132
Yam	0.226	0.051	0.076	0	0.010	0.107		0.369*
Yri	0.112	0	0	0.031	0.003	0.004	0.045*	

(b)

Monkey	Ani	Ann	Bla	Chi	Cho	Dor	Eli	Elz	Fum	Hnn	Jun	Kik	Liv	Miy	Nob	Oli	Raf	Sar	Zaz	Zin
Ani		0	0	0.136	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0.117
Ann	0.497		0	0	0	0	0	0	0.091	0	0	0	0	0	0	0.156	0	0	0	0
Bla	0	0		0	0	0	0	0	0	0.244	0	0	0	0	0	0	0	0	0	0
Chi	0	0	0		0	0	0	0	0	0	0	0	0	0	0	0	0	0.840	0	0
Cho	0	0	0	0		0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Dor	0	0	0	0	0		0	0	0	0	0.263	0	0.064	0	0	0	0	0	0	0.195
Eli	0	0	0	0	0.068	0		0.402	0	0.107	0	0	0	0.039	0	0	0	0	0.090	0
Elz	0	0	0	0.088	0	0	0.088		0	0	0	0	0	0	0	0	0	0	0	0
Fum	0.004	0.060	0	0	0	0	0	0.028		0	0	0.268	0	0	0	0.037	0	0	0	0.117
Hnn	0	0.056	0.584	0	0	0.015	0.088	0	0		0	0	0	0.052	0	0	0.510	0.325	0	0
Jun	0	0	0	0	0	0.137	0	0	0	0		0	1.145	0	0	0	0	0.028	0.131	0.331
Kik	0	0.200	0	0	0	0	0	0	0	0	0		0	0	0	0	0	0	0	0
Liv	0	0	0	0	0	0.552	0	0	0	0	0.575	0		0	0.113	0.008	0	0.041	0.234	0
Miy	0	0	0	0	0	0	0	0	0	0.078	0	0	0		0	0	0.331	0.325	0	0
Nob	0	0	0	0	0	0	0	0	0	0	0	0	0	0		0	0.020	0.008	0.031	0
Oli	0	0.515	0	0	0.020	0	0	0	0	0	0	0.008	0	0	0		0	0	0	0
Raf	0	0	0	0	0	0	0	0	0	0.180	0	0	0.181	0.062	0.919	0		0	0	0
Sar	0	0	0	0.536	0	0	0	0	0	0	0	0	0.022	0	0	0	0		0	0
Zaz	0.058	0	0	0	0	0.014	0	0	0	0	0	0	0	0	0	0	0	0		0.232
Zin	0	0	0	0	0	0.069	0	0	0	0	0.361	0	0	0	0	0	0	0	0.252	

Appendix B.16: Matrices containing the number of close approaches ($\leq$1 metre) of the groomer to the groomee during foraging, in Nina A (a) and Kw (b) group (*close-kin females in Nina A group).

(a)

Monkey	Sya	Shi	Han	Ram	Hot	Htu	Yam	Yri
Sya		0.000011	0.000011	0.000005	0	0	0	0.000005
Shi	0.000005		0.000033	0.000011	0	0	0.000011	0.000005
Han	0.000011	0.000011		0.000005	0.000016	0	0.000026	0.000005
Ram	0	0	0		0.000005	0.000005	0	0
Hot	0.000005	0	0.000016	0		0.000049*	0	0
Htu	0	0	0	0.000005	0.000016*		0	0.000011
Yam	0.000015	0	0.000010	0.000005	0.000005	0		0.000032*
Yri	0	0	0	0.000011	0.000011	0.000027	0.000005*	

(b)

Monkey	Ani	Ann	Bla	Chi	Cho	Dor	Eli	Elz	Fum	Hnn	Jun	Kik	Liv	Miy	Nob	Oli	Raf	Sar	Zaz	Zin
Ani		0.0000 19	0	0.0000 24	0	0	0	0	0	0	0	0	0	0	0	0.0000 19	0	0	0	0
Ann	0		0	0	0	0	0	0	0.0000 19	0	0	0	0	0	0	0	0	0	0	0
Bla	0	0		0	0	0	0	0	0	0.0000 21	0	0	0	0	0	0	0	0	0	0
Chi	0	0	0		0	0	0	0.0000 25	0	0	0	0	0	0	0	0	0	0.0000 99	0	0
Cho	0	0	0	0		0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Dor	0	0	0	0	0		0	0	0	0	0.0000 19	0	0	0	0	0	0	0	0	0
Eli	0	0	0	0	0	0		0.0000 39	0	0	0	0	0	0	0	0	0	0	0	0
Elz	0	0	0	0	0.0000 38	0	0		0	0	0	0	0	0	0	0	0	0	0	0
Fum	0.0000 19	0	0	0	0	0	0	0		0	0	0.0000 19	0	0	0	0.0000 19	0	0	0	0
Hnn	0	0.0000 20	0	0	0	0	0.0000 21	0	0		0	0	0	0.0000 22	0	0	0.0000 41	0	0	0
Jun	0	0	0	0	0	0	0	0	0	0		0	0.0000	0	0	0	0	0	0	0

Kik	0	0.0000 39	0	0	0	0	0	0	0	0	0	19 0	0	0	0.0000 20	0	0	0	0
Liv	0	0	0	0	0	0.0001 08	0	0	0	0	0.0000 93	0	0	0.0000 19	0.0000 19	0.0000 19	0.0000 38	0.0000 19	0
Miy	0	0	0	0	0	0	0.0000 41	0	0	0	0	0	0	0	0	0.0000 21	0	0	0
Nob	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0.0000 20	0	0
Oli	0	0.0000 79	0	0	0.0000 20	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Raf	0	0	0	0	0	0	0	0	0	0	0	0	0	0.0000 20	0	0	0	0	0
Sar	0	0	0	0.0000 25	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Zaz	0.0000 19	0	0	0	0	0	0	0	0	0	0	0	0.0000 19	0	0	0	0	0	0.0000 76
Zin	0.0000 19	0	0	0	0	0.0000 37	0	0	0	0	0	0	0	0	0	0	0	0.0000 38	

Appendix B.17: Matrices containing female agonistic support (i.e. % of aggression received by males followed by support) in Nina A (a) and Kw (b) group (*close-kin females in Nina A group).

(a)

Monkey	Sya	Shi	Han	Ram	Hot	Htu	Yam	Yri
Sya		3.6	12.1	0	0	0	0	3.0
Shi	6.3		21.2	0	0	0	0	0
Han	0	0		0	0	0	0	0
Ram	0	0	0		0	0	0	0
Hot	0	0	0	0		11.8*	0	0
Htu	0	0	0	0	0*		0	0
Yam	0	3.6	0	0	0	0		15.2*
Yri	0	0	0	0	0	0	2.5*	

(b)

Monkey	Ani	Ann	Bla	Chi	Cho	Dor	Eli	Elz	Fum	Hnn	Jun	Kik	Liv	Miy	Nob	Oli	Raf	Sar	Zaz	Zin
Ani		0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Ann	50.0		0	0	0	0	0	0	50.0	0	0	0	0	0	0	100.0	0	0	0	0
Bla	0	0		0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Chi	0	0	0		0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Cho	0	0	0	0		0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Dor	0	0	0	0	0		0	0	0	0	0	0	0	0	0	0	0	0	0	0
Eli	0	0	0	0	50.0	0		0	0	0	0	0	0	0	0	0	0	0	0	0
Elz	0	0	0	0	50.0	0	0		0	0	0	0	0	0	0	0	0	0	0	0
Fum	0	0	0	0	0	0	0	0		0	0	0	0	0	0	0	0	0	0	0
Hnn	0	0	0	0	0	0	0	0	0		0	0	0	0	0	0	0	0	0	0
Jun	0	0	0	0	0	0	0	0	0	0		0	100.0	0	0	0	0	0	0	100.0
Kik	0	0	0	0	0	0	0	0	50.0	0	0		0	0	0	0	0	0	0	0
Liv	0	0	0	0	0	0	100.0	0	0	0	33.0	0		0	0	0	0	0	0	0
Miy	0	0	0	0	0	0	0	0	0	0	0	0	0		0	0	0	0	0	0
Nob	0	0	0	0	0	0	0	0	0	0	0	0	0	0		0	0	0	0	0
Oli	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0		0	0	0	0
Raf	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0		0	0	0
Sar	0	0	0	0	0	0	0	0	0	0	0	0	100.0	0	0	0	0		0	0
Zaz	0	0	0	0	0	0	0	0	0	0	33.0	0	0	0	0	0	0	0		100.0
Zin	0	0	0	0	0	100.0	0	100.0	0	0	33.0	0	100.0	0	0	0	0	0	100.0	